

Guilford Bevil Reed

1887-1955

GUILFORD BEVIL REED, a member of the Fisheries Research Board and of its Executive since 1938, and chairman from 1947-1953, died on February 21st, 1955, after a brief illness.

Born in Nova Scotia in 1887, Dr. Reed received his primary and secondary education at Brunswick, Nova Scotia. At the age of 17 he entered the Nova Scotia Agricultural College at Truro from which he received the Diploma in Agriculture in 1907. During the next two years he was at Acadia University, from which he proceeded to Harvard. Here he spent two undergraduate and three postgraduate years. In 1912 he was given the B.Sc. degree *cum laude*, M.A. in 1913 and Ph.D. in 1915. His Ph.D. research problem concerned the respiratory enzymes. For this work he was awarded the Bowdoin Prize. In 1912 he was biologist with the Shaler Memorial Expedition which studied the geology of the Atlantic coastline.

In 1915 Dr. Reed returned to Canada as Assistant Professor of Biology at Queen's University under Professor W. T. MacClement. During the greater part of the time he held this appointment, 1915-19, he was on army leave as Captain in the Canadian Army Medical Corps. During most of the war period he was hospital bacteriologist at Queen's University Military Hospital. Later he served as bacteriologist for Military District No. 3.

In 1919 Dr. Reed was appointed Professor of Bacteriology and Head of the Department at Queen's, a position he held until his death.

From 1919 to 1940 he was consultant in Bacteriology to the Kingston General Hospital and from 1919 to 1930 consultant in Dairy Bacteriology to the Ontario Department of Agriculture.

During 1934-35 he was on leave of absence working at Cambridge University, England, and at the Pasteur Institute, Paris. At Cambridge he investigated the problem of variation and inheritance of bacteria and at Paris the serology of tuberculosis.

During the second world war Dr. Reed served as scientific consultant to the Canadian Army and as a member of the Joint American-Canadian Commission on the control of rinderpest. He was chairman of the Commission 1944-46.

He took an active part in many scientific organizations, including membership on associate committees of the National Research Council on tuberculosis, infections, food preservation and type cultures, and on the following committees of the Defence Research Board—Medical Advisory, Special Weapons, Infections, and Bacterial Warfare.

In 1947 he became director of the Kingston Laboratory of the Defence Research Board and in 1953 full-time Superintendent, a post which he held at the time of his death.

Even before being appointed a member of the Fisheries Research Board Dr. Reed had been associated with its work as an investigator. Beginning in 1921 he spent six summers at the Atlantic coast investigating problems connected with the canning of lobsters. During this period he carried out perhaps the best bacteriological work done in this field prior to the opening of the Halifax Station. He stimulated various investigators to enter the fields of the bacteriology and biochemistry of fish decomposition. In this way he may be said to have founded those aspects of the Board's work.

His great scientific knowledge which was always placed freely at the disposal of the Board made his advice in the organization and conduct of its researches of great value. He never shrank from accepting responsibilities where he thought he could be of service and his high sense of duty made him discharge every responsibility he assumed. His contributions to the effective work of the Board have been immense.

In recognition of his contributions Dr. Reed was awarded the O.B.E. in 1946, the LL.D. from the University of Saskatchewan in 1953 and from Acadia University in 1954. He was elected a Fellow of the Royal Society of Canada in 1932, was its Flavelle medalist in 1946 and President, 1952-1953. In 1947 he was awarded the United States Medal of Freedom with palm.

Dr. Reed is survived by his widow, Elsie Porter Reed, whom he married in 1915.

J. R. DYMOND

Fluctuations in Abundance of the Giant Scallop, *Placopecten magellanicus* (Gmelin), in the Digby Area of the Bay of Fundy^{1,2}

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ABSTRACT

Fluctuations in total landings and in catch per boat have characterized the Digby scallop fishery since it began in 1920. An analysis of records of the fishery indicates that, although changes in fishing methods have been partly responsible for early changes in catch, their influence in recent years has been small and changes in abundance have been primarily responsible for fluctuations in the fishery since it reached its full development in the mid-thirties.

Changes in abundance are assessed from analyses of catch records, special "census-fishing" techniques, submarine photography and marking experiments. Estimates from the different methods correspond.

Scallops are recruited into the catchable population as six-year-old year-classes. Abundance is high when these recruited year-classes are strong, but is low when they are weak. Abundance in any year is correlated with water temperature six years previously. Both abundance and the strength of individual year-classes are correlated with water temperatures which prevailed at the time the scallops were present as pelagic larvae.

It is concluded that changes in the abundance of the catchable scallop stocks result from the combined action of temperature and circulation on the pelagic larvae. Low temperatures retard larval development, and are indicative of great exchange of the water in the Bay of Fundy with outside water masses. This apparently leads to heavy losses of the larvae from the Bay, poor sets on the parent beds, weak year-classes and low abundance of the catchable stocks of six years later. High temperatures speed larval development and are indicative of a closed Fundy circulation which holds the larvae in the vicinity of the parent beds. This leads to good sets, strong year-classes and high abundance of the catchable stocks six years later.

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INTRODUCTION

FLUCTUATIONS in the abundance of both marine and terrestrial animals have been recognized as common phenomena for many years, and because of their importance in evolutionary theory (Elton, 1924) and from the practical commercial point of view (Kemp, 1938) repeated attempts have been made to understand and predict them (Dymond, 1947; Hutchinson and Deevey, 1949). Important among the detailed studies of natural populations have been those of the marine bottom fauna. Petersen (1918) showed that fluctuations in abundance occurred in the bottom fauna of two Danish fjords. Similar fluctuations of bottom fauna have been demonstrated on Dogger Bank by Davis (1925), among the oyster stocks of the Limfjord by Spärck (1927, 1949 and 1950), and for several species in the English Channel by Holme (1953). Stephen (1953) and Coe (1953) have recorded striking fluctuations among the littoral fauna. It has been concluded in these cases that fluctuations are the result of variations in the success of metamorphosis and settling, which are in turn related either directly or indirectly to the influence of hydrographic conditions on the dispersal and duration of vulnerable, pelagic larval stages. Similar explanations have been advanced for fluctuations in many species of marine fishes (Johansen, 1927; Hickling, 1935; Walford, 1938, 1946; Carruthers, 1951). Thorson (1950) found that marine, benthic, invertebrate species with a long pelagic larval life tend to show greater fluctuations of adult stock abundance than those with short pelagic larval lives, because, as he points out, success at this stage appears to be of great importance in determining adult population size, and those with long pelagic larval life are more frequently subjected to varying environmental factors which may promote or hinder development.

In recent years, fluctuations have been reported among different species of scallops (*Lamellibranchiata*) in such widely separated areas as Japan (Yamamoto, 1950), Tasmania (Fairbridge, 1953) and Georges Bank off the northeast coast of the United States (Premetz and Snow, 1953). This paper reports similar fluctuations in the abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy and concludes from the available evidence that these fluctuations are primarily controlled by the effects of water temperature and circulation on the pelagic larval stages.

ACKNOWLEDGMENTS

The writer gratefully acknowledges the assistance and encouragement he received from Dr. J. C. Medcof of the Atlantic Biological Station, who originally suggested the problem, the constructive criticisms by Dr. A. G. Huntsman during preparation of the material, and the suggestions offered by Dr. J. R. Dymond, Head of the Department of Zoology, University of Toronto, after reading the first draft. It is a further pleasure to express appreciation of the time and advice given by Dr. D. B. DeLury of the Ontario Research Foundation and Department of Mathematics, University of Toronto, in the analysis of the catch records.

The writer also wishes to thank members of the staff of the Atlantic Biological Station who helped him, notably Mr. J. S. MacPhail who assisted with field work and collection of statistics and contributed many helpful suggestions in analysis of the data, and Mrs. Ralph Lord, who assisted in compiling records of the fishery and in checking the calculations.

Special mention must be made of the kindness of Mr. E. B. Richardson, Manager of the Maritime Fish Division of National Sea Products, and Mr. Robert Archer-Shee, Manager of the Digby Packing Company who gave access to their detailed records of the fishery, and of the Digby scallop fishermen whose co-operation expedited the field work.

FLUCTUATIONS IN LANDINGS

TOTAL LANDINGS

Fluctuations in landings have characterized the fishery for scallops in the Digby area since it began in 1920. Figure 1A and Table I show the total landings of "meats" for each season.³ The data have been compiled from monthly reports submitted by officers of the Department of Fisheries. Up to 1936 the winter fishing season opened on October 16 and closed on May 31; during 1936 and 1937 it was extended to cover the period October 1 to May 31, but from 1938 to 1951 it opened on October 1 and closed April 30. The records for each of these seven- to eight-month seasons show there have been three periods of high landings, centred about the 1927-28, 1936-37 and 1945-46 fishing seasons, with intervening periods of relatively low landings.

The general trend in landings is similar to that shown during the development of many fisheries: low during the early years, a gradual increase as fishing methods were improved and the area exploited increased, and a subsequent drop to a lower level as the accumulated stocks were removed and an uneasy state of equilibrium was reached between annual production from the stocks and cropping by the fishery. When scallop fishing began in the Digby area catches were low because, at that time, small open boats using light drags fished only a small bed in the sheltered waters of Annapolis Basin (Fig. 2). About 1925, however, beds were discovered in the Bay of Fundy proper, heavier boats and

³Only the adductor muscle or "meat" of the giant scallop is used. This is shucked out by the fishermen soon after the scallops are caught and the shell and "rim", as the remainder of the soft parts is called, are discarded on the fishing ground.

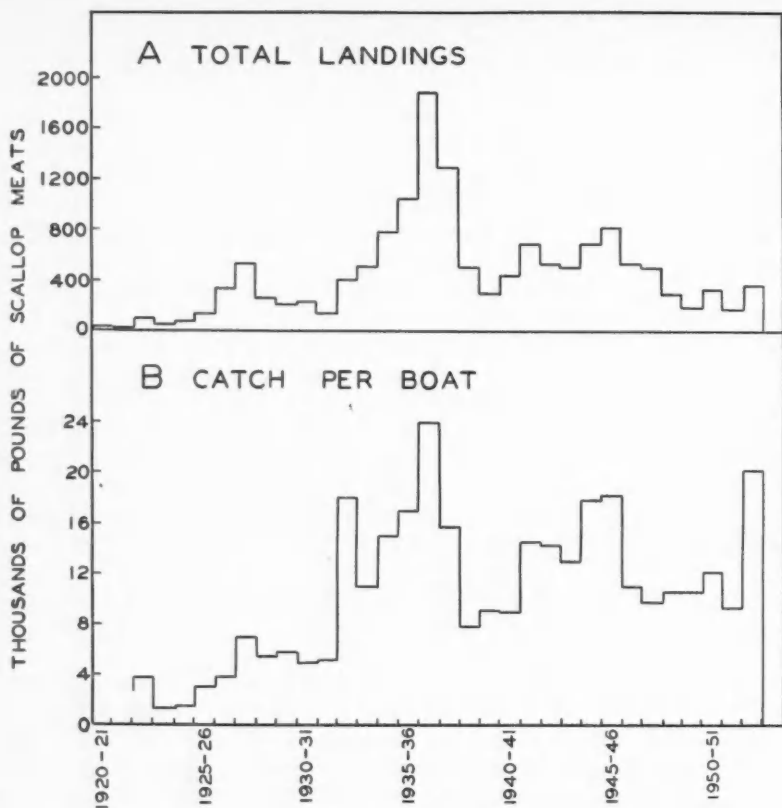


FIGURE 1. Statistics of the Digby scallop fishery.

fishing gear were developed and landings began to increase. By the mid-thirties some larger boats were operating two gangs of heavy drags having a span at the mouth of up to 30 feet. But in 1937 the total span of the gang was limited by law to 18 feet. The type of fishing gear finally developed and used by almost all draggers since 1938 has been described in detail by MacPhail (1954), and is illustrated in Figure 3.

The development of fishing methods undoubtedly contributed to the increase in landings from the beginning of the fishery through 1937 and some decrease afterwards was to be expected as fishing effort was restricted and accumulated stocks were removed. However, there were fluctuations in landings superimposed on this general picture. A peak occurred early in the fishery and another in 1945-46 after the period of high landings in 1937-38. This last peak occurred despite the fact that fishing gear has remained much the same, and no new beds

TABLE I. Catch statistics and fleet size of the Digby scallop fishery. The "additional statistics" in column 4 were supplied by Mr. E. D. Fraser, formerly Chief Supervisor of Fisheries Eastern Division, Canada Department of Fisheries.

Year	Total landings Oct.-Apr., inc.	Fleet size estimated from			Actual count	Fleet size (best estimate)	Average seasonal catch per boat
		Published fisheries statistics	Additional statistics	Customs clearance			
1920-21	34,600	...					
1921-22	28,600	...					
1922-23	79,100	22				22	3,600
1923-24	57,900	48				48	1,200
1924-25	69,200	48				48	1,400
1925-26	131,500	48				48	2,700
1926-27	329,600	90				90	3,700
1927-28	535,800	78				78	6,900
1928-29	249,400	45				45	5,500
1929-30	199,100	35				35	5,700
1930-31	225,400	43				43	5,200
1931-32	122,700	23				23	5,300
1932-33	411,600	...	23			23	17,900
1933-34	511,000	...	46			46	11,100
1934-35	766,000	...	52			52	14,700
1935-36	1,066,500	...	63			63	16,900
1936-37	1,854,300	69	78			78	23,800
1937-38	1,276,700	70	82			82	15,600
1938-39	506,700	66				66	7,700
1939-40	308,800	34				34	9,100
1940-41	447,100	50				50	9,000
1941-42	682,100	47				47	14,500
1942-43	552,200	39				39	14,200
1943-44	493,500	38				38	13,000
1944-45	694,300	39				39	17,800
1945-46	842,300	46				46	18,300
1946-47	535,100	46	48	49		49	10,900
1947-48	449,200	40		47		47	9,600
1948-49	275,800	35	33	26		26	10,600
1949-50	179,400	25	27	17		17	10,600
1950-51	333,200		33	27		27	12,300
1951-52	169,400		21	16	18	18	9,400
1952-53	366,700				18	18	20,400

have been found or exploited since the mid-thirties. Such fluctuations in total landings suggest that there have been fluctuations in the abundance of the stocks, and this is supported by a consideration of the seasonal catch per boat.

CATCH PER BOAT

Records of fleet size have been obtained from several sources and are given in Table I. For the years 1920 to 1931 and 1938 to 1945, inclusive, the published reports in Fisheries Statistics of Canada of the number of scallop licences issued are the only records available and they have been used. Between 1931 and 1938 special records of licences issued were kept by an officer of the Department of Fisheries, and these have been used. But licences are issued for the fiscal year April 1 to March 31 which overlaps the fishing season, and recent observations have shown that, because of the overlap, the number of licences issued for any

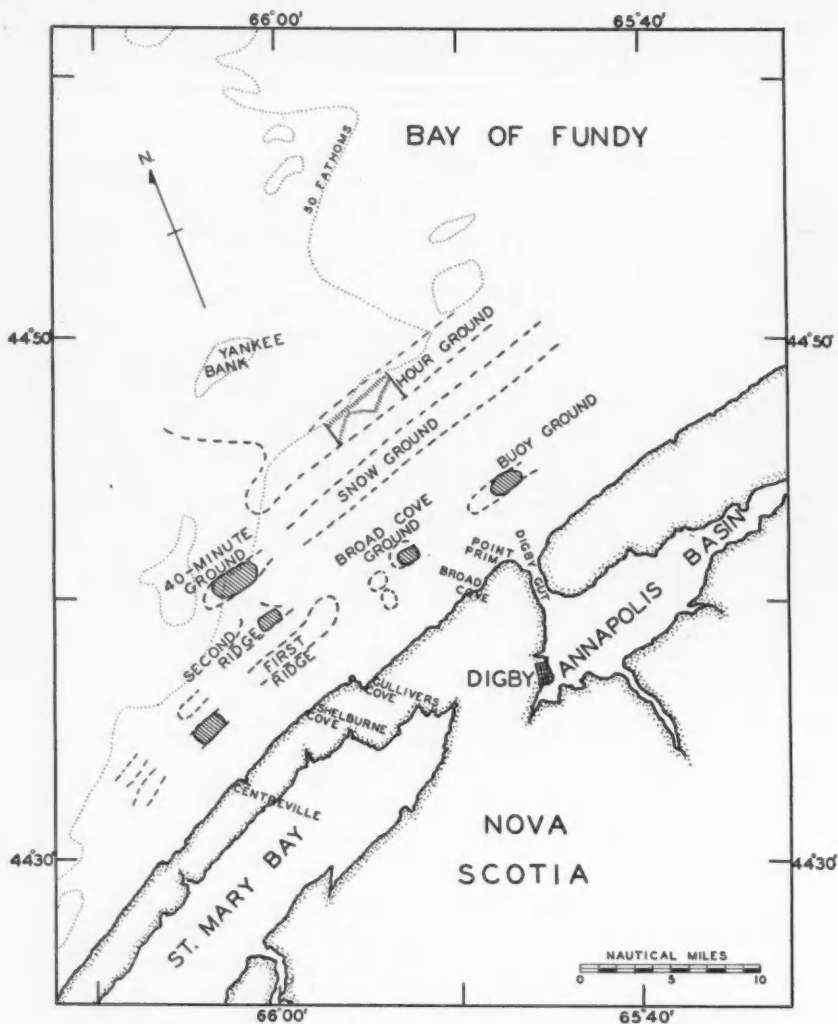


FIGURE 2. The Digby area of the Bay of Fundy, showing the principal scallop beds. Dashed outlines indicate approximate boundaries of the beds; shaded areas represent regularly censused beds.

fiscal year tends to give an overestimate of the fleet size for the most early corresponding season, particularly during periods when fleet size is decreasing. For this reason the more reliable Canadian Customs records of boats clearing for scallop fishing have been used since they became available in 1946, except for the 1951-52 and 1952-53 seasons when actual counts of the fleet were made.

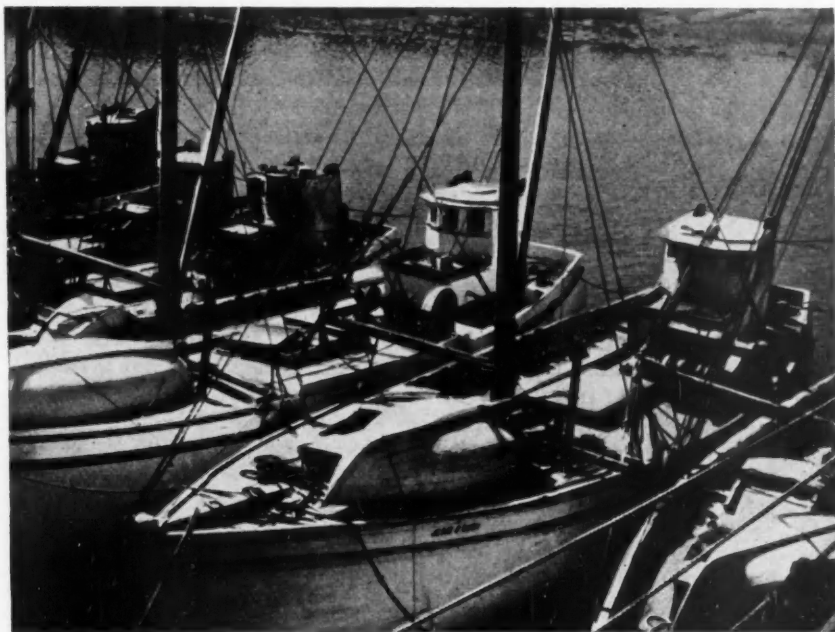


FIGURE 3. Typical Digby scallop draggers.

These records, despite certain weaknesses, show the order of size of the fleet and reflect the principal changes in it from season to season.

Records of total landings and fleet size have been used to calculate average catch (landings) per boat per season which is given in Table I and Figure 1B. The gradual rise from the beginning of the fishery until 1937 again reflects, in part at least, changes in the availability of scallops through the development of more efficient fishing methods and expansion of the area exploited. But fluctuations occur in catch per boat at the same times and are more marked than fluctuations in total landings.

Since fishing efficiency became stabilized about 1937, subsequent fluctuations in catch per boat strongly suggest changes in abundance of the exploited stocks. This is further supported by the following analysis, where measures of abundance changes are made from special fishing records combined with the information from Fisheries Statistics.

CALCULATIONS OF ABUNDANCE CHANGES

Abundance may be judged in several ways from the data on hand. These include estimates of relative abundance from the Fisheries Statistics and from special detailed catch statistics for a sample fleet, as well as calculations of actual abundance from the Fisheries Statistics combined with sets of special statistics, and from the results of a strip-census by special fishing.

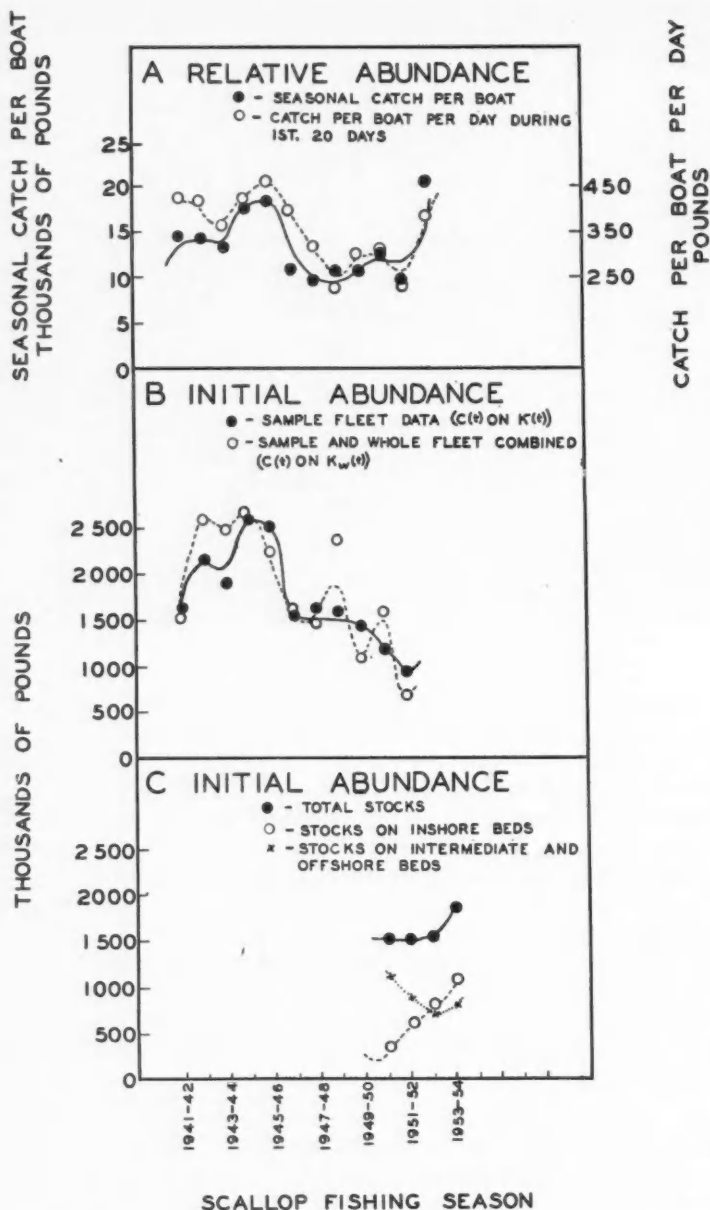


FIGURE 4. Estimates of abundance of the Digby scallop stocks.

RELATIVE ABUNDANCE

Seasonal catch per boat, used above as a rough measure of changes in relative abundance from 1937 to the present, is shown in Figure 4A for the period 1941-42 to 1952-53 inclusive. It is generally recognized, however, that catch during any one season may be influenced by factors other than abundance alone, some of which are illustrated by the following analysis.

Records of the daily landings of a number of boats are available, beginning with the 1941-42 fishing season. From them a sample composed of five of the boats fishing during each of the 12 seasons from 1941-42 to 1952-53, inclusive, has been selected. Although the composition of the sample fleet has changed from time to time, it has been possible in most cases to substitute for any boat which ceased fishing another of approximately the same performance. The data are given in detail by Dickie (1953).

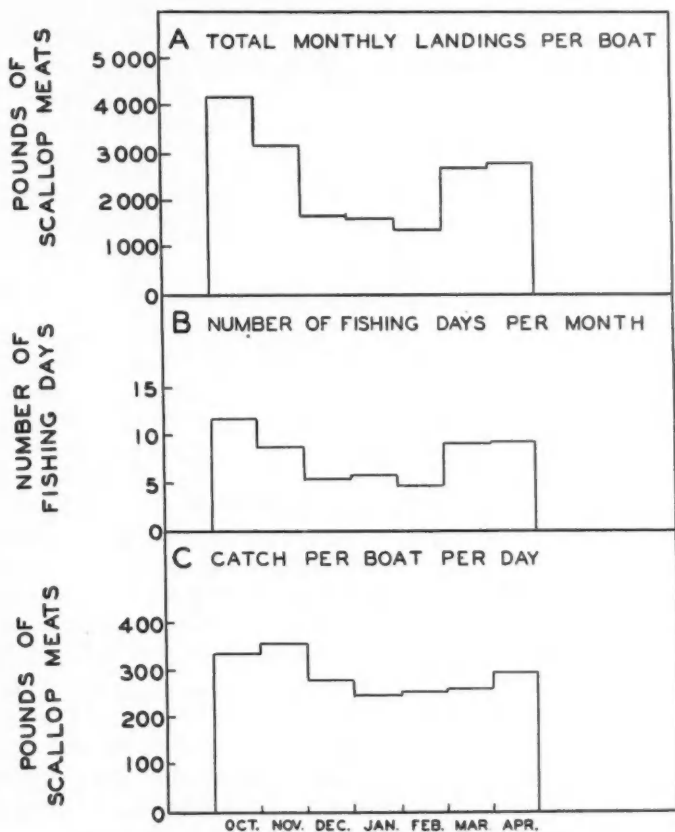


FIGURE 5. Month to month changes in the Digby scallop fishery.

SEASONAL VARIATION IN CATCH

Figure 5A summarizes the 12 years' special statistics to show how catch per boat varied from month to month during the seven-month fishing season. An average seasonal catch of 17,885 pounds was taken by each of the sample boats of which 43 per cent (7,724 lb.) was taken in the first two months combined, 26 per cent (4,701 lb.) in the three mid-winter months, and 34 per cent (5,460 lb.) in the last two. This variation can be explained as resulting from changes in weather conditions and abundance.

INFLUENCE OF WEATHER

Although there are potentially 212 or 213 days in each season, and the boats go out whenever the weather is fit (except Sundays) an average of only 56 fishing days per season was realized by each. Figure 5B shows that 37 per cent (21 days) occurred in the first two months, 29 per cent (16 days) in the three mid-winter months and 34 per cent (19 days) in the last two. The correspondence between monthly catch and days fished per month (correlation coefficient of 0.941) indicates that weather is the major factor producing month to month catch variation within each season.

INFLUENCE OF ABUNDANCE CHANGES

In view of the influence of weather on the season's catch, average catch per boat per day may be regarded as a better index of abundance than averages taken over a longer period because, unless the lengths of fishing days change greatly, it will go up or down depending on whether the beds fished are well or poorly stocked. Average catch per boat per day in each month of the season is shown in Figure 5C. It suggests that there are abundance changes within each season. There is a mid-winter depression in catch which may be attributed in part to the shortness of winter fishing days and unsettled weather rather than to abundance changes alone, but the important feature is a drop in average daily catch in March and April to only about 80 per cent of that in October and November, although the lengths of fishing days in these two periods are approximately the same. An analysis of covariance (see Appendix) indicates that the difference in catch per boat per month during the first two and last two months of the 12-year period is statistically significant, independent of changes in the size of the catches in different years. Grouping into averages in this way is, therefore, legitimate, and the difference between the first and last of the season indicates that catch within the season is influenced by a decrease in abundance which must result from the combined effects of fishing and natural mortality.

INDICES OF RELATIVE ABUNDANCE

It must be concluded that seasonal catch per boat in Figure 4A may be an unreliable index of relative abundance because of possible changes from one season to another in the magnitude of the influence of weather or of removals by natural and fishing mortalities on the catch. A better index would be average catch per boat per trip during the early part of the season (cf. Ricker, 1940).

Such data are not available for the whole fleet, but can be obtained for the sample fleet from the special statistics. Figure 4A also shows average catch per boat of the sample fleet per day during the first 20 fishing days of each season.

Figure 4A shows that the trend in relative abundance judged from statistics of the sample fleet corresponds closely with that obtained from statistics for the whole fleet (correlation coefficient of 0.823 for the 12-year period), although there are several discrepancies between them. Such discrepancies may be largely a result of the fact that the boats used for the sample were "high-liners", that is, the best fishermen of the fleet rather than a representative sample, and that they formed a variable proportion of the total as fleet size changed from year to year. In addition, the composition of the sample fleet itself has changed from year to year and this will undoubtedly affect the relative size of its catches, despite efforts to select boats of approximately the same performance throughout. Changes of this sort have occurred in the sample fleet used from 1946-47 to 1952-53 and there was a complete change in the boats used between 1947-48 and 1951-52.

Despite weaknesses in data on catch per unit effort as bases for estimates of relative abundance, it must be concluded from the correspondence between these two indices that abundance rose from 1941-42 to a maximum about 1945-46, decreased sharply afterwards, but increased again in 1952-53. This conclusion may be checked, and both sets of values for relative abundance criticized by comparing them with the results of other methods of calculation which can be checked by independent special fishing data.

ACTUAL ABUNDANCE FROM DETAILED CATCH DATA

The technique for estimating population size from detailed data on catch, or by sampling and removal, has been developed and described by DeLury (1947, 1951) who used it for calculating populations of trout and lobsters. It has been used for the analysis of creel census data by Mottley (1946), and for the estimation of populations of small mammals by Haynes (1949); Gerking (1952) and Ketchen (1953) have compared estimates from this method with population estimates derived from the more familiar Schnabel and Petersen tagging techniques.

METHODS OF CALCULATION

DeLury has shown that if a population is subjected only to fishing, if the units of fishing gear do not compete at any one instant, and if catchability (defined as the fraction of the population removed by a unit of effort) is constant, then the change in catch per unit effort can be used to calculate actual initial population. Using his symbols, by definition:

$$C(t) = kN(t)$$

where $C(t)$ is the catch per unit of effort during any short interval of time, k is the constant catchability, and $N(t)$ is the population present at the beginning of the catching interval. That is, catch per unit of effort is proportional to population present. If decreases in this population are the result of fishing alone,

the population present at any time—"N(t)"—is equal to the initial population—"N(0)"—less the total catch up to that time—"K(t)". That is:

$$N(t) = N(0) - K(t).$$

Substituting this equation in the first:

$$\begin{aligned} C(t) &= k\{N(0) - K(t)\} \\ \text{or} \quad C(t) &= kN(0) - kK(t) \end{aligned} \quad (1)$$

Therefore, if the catch per unit effort during successive short intervals of time is plotted against total catch up to each of these intervals and the assumptions hold, the points will fall along a straight line. An estimate of initial population may be calculated from the slope— k —and the intercept of the line on the ordinate— $kN(0)$.

Conditions for fitting this simple equation are rarely met in nature. In some cases catchability may change during a season, or the population may be subject to changes resulting from natural mortality or growth. Furthermore, detailed data of the kind required are rarely available for all the effort of large fisheries. In the case of the scallop fishery, catch from day to day may be influenced by weather giving rise to catchability changes, and natural mortality of the stocks probably takes place, so that the assumption of no natural mortality would be unrealistic. The major part of scallop growth takes place during the summer and only the end of the growing season overlaps the winter fishing season, so that the assumption of no significant changes in population from growth is justified. But detailed catch data are available for only a sample of the total fleet.

DeLury (1951) has shown how the basic equation may be expanded to take some of these situations into account. For example, when two kinds of effort are operating on a population, the equation fitted is approximately (cross product terms neglected):

$$C(t) = kN(0) - \left(\frac{k + k'e'}{e} \right) K(t) \quad (2)$$

where $C(t)$ and $K(t)$ are the catch per unit effort and accumulated catch of a certain sample of the total effort, k and e are the catchability and effort which may be assigned to this sample, and k' and e' are the corresponding values for the remainder of the effort. That is, if catch per unit of effort— $C(t)$ —of a sample fleet is plotted against accumulated catch of this sample— $K(t)$ —the resulting straight line has a slope \hat{k} which reflects not only the drain of the sampled effort on the population but also the drain imposed by the remainder of the effort.

If more than two kinds of effort are involved the equation becomes:

$$C(t) = kN(0) - \left(k + \frac{k'e'}{e} + \frac{k''e''}{e} \right) K(t) \quad (3)$$

where k'' and e'' are the catchability and effort of the third kind of effort. If it is identified with natural mortality, k'' is the instantaneous natural mortality rate

on the basis of one day as a unit of time and e'' is the number of days for which it operates. The product $-k''e''$ is therefore the instantaneous natural mortality rate applying over the fishing season.

In order to apply these equations to the scallop data several calculations must be made. These include: (1) the calculation of a unit of effort which does not change in efficiency during the season (i.e. constant catchability), (2) the calculation of the ratio of the catchabilities and efforts of the sampled and unsampled parts of the fleet to be used as correction terms, (3) the calculation of a correction term for natural mortality.

(1) CALCULATION OF CATCH PER UNIT OF EFFORT— $C(t)$. Weather influences the catch in each month (p. 806) and our experience with the fishery has shown that it is virtually impossible to fish when wind velocities exceed 15 miles per hour. When they are between 10 and 15 m.p.h., long enough to raise waves, catches are small because handling the drags is difficult and dangerous, and in the fishermen's opinion rough water lowers catches because the drags skip over the bottom. Calm weather is necessary for fully effective fishing. It follows that if average catch per boat per day is used as a unit of effort, weather changes will lead to changes in catchability from day to day throughout the season and abundance cannot be accurately calculated from the catch data.

Fine and poor fishing days can be determined with some accuracy from records of wind velocity kept by the Meteorological Observation Station at Greenwood, N.S. The wind velocity for each day was obtained from the original records. From a knowledge of the habits of the fishermen, it was decided that a fit fishing day might be defined as one on which from midnight to noon the wind velocity did not exceed 10 m.p.h. and either remained calm or did not exceed 15 m.p.h. until the succeeding midnight.

To eliminate bias in the analysis, only catches made on days which could be defined as fine from meteorological records were used in calculating catch per unit of effort, and all others were disregarded, with two exceptions. The first exception was made if on an apparently fine day one or more of the boats failed to land but reported on the succeeding day. The late report was taken to indicate that the boat arrived at the wharf after the fish plants closed so that its catch the second day was counted as a fine day's catch regardless of weather that day. If the weather on the second day was also fine and the catch of the formerly missing boat was double, or nearly double, that of boats landing on either or both days, its catch was counted as two days' catch. The second exception was made if the catch of one of the boats, on an apparently fine day, was very much lower than catches made by other boats on that day, or was much lower than that boat's usual performance would indicate it could have made. Such low catches were assumed to have resulted from engine or similar trouble. An examination of the records indicated that for the sample fleet boats all fine-day catches of less than 150 pounds might be regarded as abnormally low and this was taken as the lower limit of catches used in calculating average catch per boat per fine day.

Using the weather data to define fine fishing days, the average catch per boat per fine day was determined for each week of each season. A week was chosen as the most natural interval into which a season may be divided, as scallop fishing, like many other human activities, is based on a weekly cycle. Following this line of reasoning, the catch per unit effort for the scallop fleet was defined as weekly average catch per boat per fine fishing day. The data available for the sample fleet, and the selection to represent catch per unit effort are given in detail by Dickie (1953).

(2) CALCULATION OF THE CORRECTION TERM: $\frac{k'e'}{ke}$. When catch per unit of

effort of a sample of the total effort acting on a population— $C(t)$ —is plotted against the accumulated catch of this sample— $K(t)$ —the regression line so obtained is of the form:

$$C(t) = kN(0) - \hat{k} K(t) \quad (2) \text{ (p. 808)}$$

and the abscissal intercept and slope give estimates of $kN(0)$ and \hat{k} respectively. Since the sample fleet statistics alone have been used to calculate these lines, the observed slope is a compound, including the effects of both the sampled and unsampled fleets. That is,

$$\hat{k} = k + \frac{k'e'}{e} = k \left(1 + \frac{k'e'}{ke} \right),$$

where k and e refer to the sample fleet and k' and e' to the unsampled fleet. From this the true catchability is:

$$k = \hat{k} \left(\frac{1}{1 + \frac{k'e'}{ke}} \right).$$

The ratios k'/k and e'/e may be obtained from the ratios of the catches of the two fleets. Since by definition catch per unit effort of the sample fleet $= C(t) = kN(t)$ and catch per unit effort of the whole fleet $C'(t) = k'N(t)$, the ratio:

$$\frac{C'(t)}{C(t)} = \frac{k'N(t)}{kN(t)} = \frac{k'}{k}.$$

That is, the ratio of the catchabilities is the same as the ratio of catches per unit of effort. The efforts of the two fleets are represented by e and e' . If it is assumed that the ratio of the effort of the sampled and unsampled portions of the fleet was constant throughout the season,

$$\frac{e'}{e} = \frac{\text{size of the unsampled fleet}}{\text{size of the sampled fleet}} = \frac{\text{Fleet (u)}}{\text{Fleet (s)}}.$$

Combining these ratios to give the denominator of the correction factor,

$$\begin{aligned} \frac{k'e'}{ke} &= \frac{\frac{\text{Total } K'(t)}{\text{Fleet (u)}}}{\frac{\text{Total } K(t)}{\text{Fleet (s)}}} \times \frac{\text{Fleet (u)}}{\text{Fleet (s)}} = \frac{\text{Total } K'(t)}{\text{Total } K(t)} \\ &= \frac{\text{Total catch of the unsampled fleet}}{\text{Total catch of the sampled fleet}} \end{aligned}$$

That is, the correction factor is dependent only upon the ratio of the catches of the two parts of the fleet and is equivalent to considering the accumulated catch of the sample fleet as a given and constant fraction of the accumulated catch made by the unsampled fleet during the same period.

(3) CALCULATION OF THE RATE OF NATURAL MORTALITY. Shells of scallops which have recently died from natural causes can be distinguished from those killed by the fishery. In shucking, the two valves of the shell are always separated before the adductor muscle or meat is removed and the shells are discarded on the bed. Natural mortality, on the other hand, leads to decomposition or removal of the soft body parts and leaves the two valves firmly attached by the hinge ligament. These empty shells persist for some time before the hinge ligament decomposes and the valves separate. Numbers of the empty shells, called "cluckers" by the fishermen, are brought up in the drags along with living scallops, single shells and detritus.

The rate of natural mortality can be estimated from the relative size of the populations of living scallops and cluckers. The population of cluckers may be regarded as a "pool" of dead animals to which newly dead animals are constantly added and from which the separating cluckers are removed. If, over a given period of time, the size of this dynamic pool remains constant, the number of scallops dying must be just balanced by the decomposition of cluckers, and the numbers of living scallops which die per unit time may be determined from the rate of decomposition of cluckers. The number dying per unit time, expressed as a fraction of the average population of living, gives an estimate of the natural mortality rate.

The size of the population of living scallops and cluckers may be judged from the catches of each made in a series of tows of standard length on each of several beds during the summers of 1950, 1951 and 1952. Since few cluckers of less than 96 mm. in shell height were taken, natural mortality rate is determined principally from the larger size-groups. Part I of Table II shows the average number per tow of living and cluckers of 96 to 155 mm. in shell height. Part II shows similar records for those of less than 96 mm. If living scallops and cluckers are equally liable to capture by scallop gear, the average number of each taken per tow is a reflection of the relative population size.

Within the limits of sampling error illustrated by catch variations on 40-Minute Ground in a six-day period from September 4 to September 9, 1950, the population appears to have remained constant over a period of almost a

month. Furthermore, the relative numbers of living and dead per tow on Buoy Ground, Broad Cove and 40-Minute Ground remained about the same throughout the sampling period of two years. The Shelburne Cove and Offshore Ground show more variation, although the latter was much the same in 1951 and 1952. From these samplings it may be tentatively concluded that throughout the period of observations, additions to the clucker population through natural death of scallops have been balanced by decomposition of the cluckers.

A preliminary tank experiment to determine the rate of separation of clucker shells of different sizes was carried out by Dr. J. C. Medcof and Mr. J. S. MacPhail of the Atlantic Biological Station. They kindly allowed the writer to use their unpublished results which, for the purposes of estimating natural mortality, were grouped to give average time from death of scallops to separation of valves of cluckers of less than 96 mm. and between 96 and 155 mm. in shell height. Average time to separation in the smaller cluckers was 51.4 days and for the larger was 103.4, or about 50 and 100 days. The daily rate of separation of cluckers is, therefore, 1/50 and 1/100, for small and large respectively.

Natural mortality rate was calculated from these data as follows: On Buoy Ground in 1950 an average of 1.375 large cluckers was taken per standard tow. The rate of separation of cluckers was therefore $1.375 \times 1/100 = 0.01375$ cluckers per day. The average number of living scallops taken in the same tows was 75.88. From this $0.01375/75.88 = 0.0001812$ of the scallops present per unit area die from natural causes each day. The daily natural mortality rate may be converted to an annual mortality rate (cf. Ricker, 1944) from the relationship:

$$a = 1 - e^{-it}$$

where a is the annual mortality rate, e is the natural base of logarithms, i is the instantaneous (i.e. daily) natural mortality rate, and t is the number of days. If a is to be determined over a year, then $t = 365$ days, and the annual natural mortality rate for Buoy Ground in 1950 is:

$$\begin{aligned} a &= 1 - e^{-(0.0001812)(365)} \\ &= 1 - e^{-0.0661} \\ &= 1 - 0.9361 = 0.0639. \end{aligned}$$

Natural mortality rate was calculated in this way for each scallop bed in each season and the results are shown in Table II.

The results of the calculations show that natural mortality rate is relatively constant for the same bed from year to year, but the beds appear to fall into three quite distinct groups. The first, including Buoy Ground and Broad Cove Ground, two beds in 40 to 45 fathoms of water close to Digby Gut, have a low annual natural mortality rate of only about 4.5 per cent. The Shelburne Cove and 40-Minute Ground, two areas situated near the western end of the scallop area in about 50 fathoms of water, suffer annual natural mortalities of about 13.8 per cent, while the offshore beds, in 55 fathoms, have an annual natural mortality of about 15.7 per cent.

The catches of scallops landed at Digby, N.S., do not come equally from the areas which exhibit these different natural mortality rates, so that no one rate is appropriate as a correction factor in calculations of abundance. However,

TABLE II. Relative populations of living and clucker scallops and calculation of natural mortality from the relationship between them.

Scallop bed	Year	No. of hauls	No. of cluckers per haul D	No. of living per haul P	No. of days cluckers persist L	$\frac{D}{L} \times \frac{1}{P}$ $= i$	it ($t = 365$ days)	e^{-it} $= s$	Annual natural mortality rate $\alpha = 1 - s$
Part 1—96- to 155-mm scallops									
Buoy Ground	1950	8	1.375	75.88	100	.0001812	.0661	.9361	.0639
	1951	4	0.875	141.46	100	.0000619	.0226	.9773	.0227
	1952	11	1.591	91.75	100	.0001735	.0633	.9390	.0610
Broad Cove	1951	5	1.167	108.27	100	.0001080	.0394	.9628	.0372
	1952	6	0.972	96.64	100	.0001006	.0367	.9637	.0363
Shelburne Cove									
1st Ridge	1950	9	6.333	131.56	100	.0004814	.1757	.8386	.1614
2nd Ridge	1950	4	9.600	163.30	100	.0005879	.2146	.8069	.1931
2nd Ridge	1952	4	3.792	164.50	100	.0002305	.0841	.9194	.0806
40-Minute, Ground									
Aug. 14	1950	10	10.600	247.40	100	.0004285	.1564	.8556	.1444
23	1950	9	10.111	332.56	100	.0003040	.1110	.8949	.1051
24	1950	9	13.111	344.33	100	.0003808	.1390	.8705	.1295
Sept. 4	1950	3	15.667	269.67	100	.0005810	.2121	.8090	.1910
6	1950	8	11.875	328.13	100	.0003619	.1321	.8763	.1237
8	1950	11	11.000	271.18	100	.0004056	.1480	.8624	.1376
9	1950	3	13.000	252.67	100	.0005145	.1878	.8286	.1714
	1951	9	10.630	280.51	100	.0003789	.1383	.8711	.1289
	1952	11	10.394	194.31	100	.0005349	.1952	.8229	.1771
Offshore									
Inner	1950	9	42.000	602.00	100	.0006977	.2547	.7749	.2251
Outer	1950	6	29.750	610.75	100	.0004871	.1778	.8370	.1630
Inner	1951	4	10.500	277.96	100	.0003778	.1379	.8711	.1289
Inner	1952	6	8.063	234.57	100	.0003463	.1264	.8816	.1184
Part 2—0- to 95-mm scallops									
Buoy Ground	1952	11	1.390	195.69	50	.0001420	.0518	.9493	.0507
Offshore									
Inner	1950	9	4.375	220.15	50	.0003975	.1451	.8650	.1350
Outer	1950	6	4.669	180.85	50	.0005163	.1885	.8278	.1722

Av. Buoy Gr. and Broad Cove = $0.0453 = 4.5\%$.Av. Shelburne Cove and 40-Minute Ground = $.1377 = 13.8\%$.Av. Offshore = $.1571 = 15.7\%$.

what is known of the fishery indicates that roughly half of the total catch regularly comes from Buoy Ground and Broad Cove combined, about one-third from the rest of the inshore areas and the remainder from offshore (until very recently when a greater proportion came from offshore). On this basis, the natural mortality of the fished population is:

$$0.50 \times 0.045 = 0.0225$$

$$0.30 \times 0.138 = 0.0414$$

$$0.20 \times 0.157 = 0.0314$$

$$\text{Total} = 0.0953.$$

Thus the average rate is about 10 per cent per year.

This estimate of annual natural mortality is obviously subject to considerable error. It is based on sampling data which show considerable variation, and on estimates of rate of separation of shells from preliminary experiments. More important than these, however, are some field observations reported by Chiasson (1952). He observed a mass mortality of scallops in Northumberland Strait in 1950, and his measurements of cluckers and living showed that the modes in the size-distribution of the two corresponded. On re-examination of the same bed in 1951 he found large numbers of cluckers which had a size-distribution corresponding with that of the previous year while the modes in the size-distribution of the living were greater by an amount expected on the basis of annual growth. His conclusions that the 1951 cluckers represent 1950 deaths seems justified and shows that cluckers in Northumberland Strait may persist much longer than did shells held in the tanks at St. Andrews. In the Digby collections the modes in the size-distribution of living scallops and cluckers correspond, indicating that cluckers do not persist as long in the Bay of Fundy as in Northumberland Strait. However, there remains the possibility that they persist longer in the Bay of Fundy than they did in the tank experiments. If this should prove true, the rate of natural mortality estimated above is too high.

Although an average annual 10 per cent mortality rate has been assigned to the stocks, observations on which this is based were made during middle and late summer (July to September). If natural mortality results from depredations by starfish and gastropods (which are common on and around the Digby scallop beds), one would expect it to be highest in September and October when the bottom water of the Bay of Fundy is warmest and predators are most active. Therefore, the mortality rate, calculated from observations made in August and September, is likely to be near the annual maximum.

It may be concluded that the annual natural mortality rate of the fished population of Digby scallops is of the order of 10 per cent and is not likely to greatly exceed this value.

An annual rate of 0.10 corresponds with an instantaneous rate of 0.1054. The instantaneous rate for the scallop season which lasts for 212 days is $0.1054 \times 212/365 = 0.0613$, and the corresponding "annual" (i.e. for the scallop season) rate is $1 - e^{-0.613} = 1 - 0.9406 = 0.0594$ or approximately 6 per cent.

From the earlier discussion of methods it was shown that when the sampled and unsampled fleet and natural mortality are all acting on the population, catch per unit effort of the sample fleet plotted against the sample fleet's accumulated catch gives a straight line with observed slope $\hat{k} = k + k''e''/e$ where the product $k''e''$ is the seasonal rate of natural mortality, or 0.060. The denominator of the fraction $k''e''/e$ is the effort expended by the sample fleet during the same time. Since the sample fleet is composed of five boats, it is five times the number of units of effort by each boat—i.e. $5 \times$ average number of days fished per boat in each year.

ABUNDANCE ESTIMATES

With an appropriate catch per unit of effort and corrections for sample catch statistics and natural mortality, two methods may be used to plot the

catch data for estimating abundance: (1) The sample fleet's catch per unit effort may be plotted against its accumulated catch and the estimate of $N(0)$ so obtained corrected to take the unsampled effort and natural mortality into consideration, or (2) the sample fleet catch per unit effort may be plotted directly against the accumulated catches of the whole fleet and the result corrected for natural mortality alone.

The two methods can be shown to be mathematically equivalent if in any one season the sample fleet effort and catches are a constant proportion of effort and catches by the whole fleet. For example, it was shown above (p. 808) that if catch per unit effort of a sample fleet— $C(t)$ —is plotted against the accumulated catch made by the same boats, the result is a straight line of the form:

$$\begin{aligned} C(t) &= kN(0) - \left(k + \frac{k'e'}{e}\right)K(t) \\ &= kN(0) - k\left(1 + \frac{k'e'}{ke}\right)K(t). \end{aligned} \quad (2)$$

If k' and e' , and k and e , are the catchabilities and efforts of the unsampled and sampled fleets respectively, then from the definition of terms, the total effect of the whole fleet on the population is approximately equal to the sum $k'e' + ke$ over a given interval of time. The proportion of this total which may be assigned to the sample fleet alone is then:

$$\frac{ke}{k'e' + ke}.$$

The proportion of the catch of the whole fleet— $K_w(t)$ —which is taken by the sample fleet will be:

$$K(t) = \frac{ke}{k'e' + ke} K_w(t).$$

From this relationship:

$$\begin{aligned} K_w(t) &= \frac{k'e' + ke}{ke} K(t) \\ &= \left(1 + \frac{k'e'}{ke}\right) K(t). \end{aligned} \quad (4)$$

Substituting in equation (2)

$$C(t) = kN(0) - kK_w(t). \quad (5)$$

Therefore abundance estimates obtained from plotting catch per unit of effort by the sample fleet against its accumulated catch and correcting the apparent catchability for the effect of the unsampled effort are equivalent to estimates obtained directly from plotting catch per unit effort of the sample against the accumulated catch of the whole fleet.

Similarly, the expanded form of the DeLury equation:

$$C(t) = kN(0) - \left(k + \frac{k'e'}{e} + \frac{d''e''}{e} \right) K(t) \quad (3)$$

(p. 808) may be written in the form:

$$C(t) = kN(0) - k \left(1 + \frac{k'e'}{ke} \right) K(t) - \frac{k''e''}{e} K(t)$$

In this equation the values of $K_w(t)$ may be substituted directly for $K(t)$ from the relationship in (4) above to yield the equation:

$$\begin{aligned} C(t) &= kN(0) - kK_w(t) - \frac{k''e''}{e} \left(\frac{1}{1 + \frac{k'e'}{ke}} \right) K_w(t) \\ &= kN(0) - \left\{ k + \left(\frac{k''e''}{e} \right) \left(\frac{1}{1 + \frac{k'e'}{ke}} \right) \right\} K_w(t) \end{aligned} \quad (6)$$

In equation (6) the apparent catchability differs from the true catchability because natural mortality, expressed as a fraction of the effect of the *whole* fleet, has taken place. The calculation of the correction terms is given in Table III.

TABLE III. Calculation of correction terms for estimating abundance from catch statistics. See text, pages 810-811 and 814-816, for derivations of the terms.

Season	Total landings		Correction of regression for total fleet $1 + \frac{k'e'}{ke} = 1 + \frac{C(u)}{C(s)}$	Seasonal natural mortality $k''e''$	No. sample boats	No. days fished	Product e	Correction for natural mortality $= \frac{k''e''}{e}$
	Sampled fleet $C(s)$	Unsampled fleet $C(u)$						
1941-42	134,842	547,208	5.0581	0.0600	5	78.6	393	0.0001527
1942-43	114,023	438,127	4.8424	0.0600	5	62.4	312	0.0001923
1943-44	100,436	393,064	4.9136	0.0600	5	61.0	305	0.0001967
1944-45	130,477	563,783	5.3204	0.0600	5	64.0	320	0.0001875
1945-46	111,353	730,897	7.5638	0.0600	5	62.2	311	0.0001929
1946-47	79,675	455,425	6.7160	0.0600	5	54.6	273	0.0002198
1947-48	65,419	383,781	6.8665	0.0600	5	50.8	254	0.0002362
1948-49	47,269	228,531	5.8347	0.0600	5	42.4	212	0.0002830
1949-50	56,666	121,234	3.1395	0.0600	5	45.4	227	0.0002643
1950-51	61,922	271,278	5.3810	0.0600	5	47.8	239	0.0002511
1951-52	44,508	124,892	3.8061	0.0600	5	41.2	206	0.0002913

The data needed for fitting each form of the equation are available for the 11-year period 1941-42 to 1951-52 inclusive, and both methods have been used for arriving at abundance estimates.

(1) Estimates of abundance based on the regression lines drawn from the data for the sample fleet alone are given in Figure 4B, and the regression lines in Figure 6. (See Table IVA for details of the calculations.) They indicate that the scallop "meats" present before the fishing season in 1941-42 weighed about 1.6 million pounds, increased in 1942, but dropped to 1.8 million pounds in 1943, and rose to 2.6 and 2.5 million pounds in 1945 and 1946, respectively.

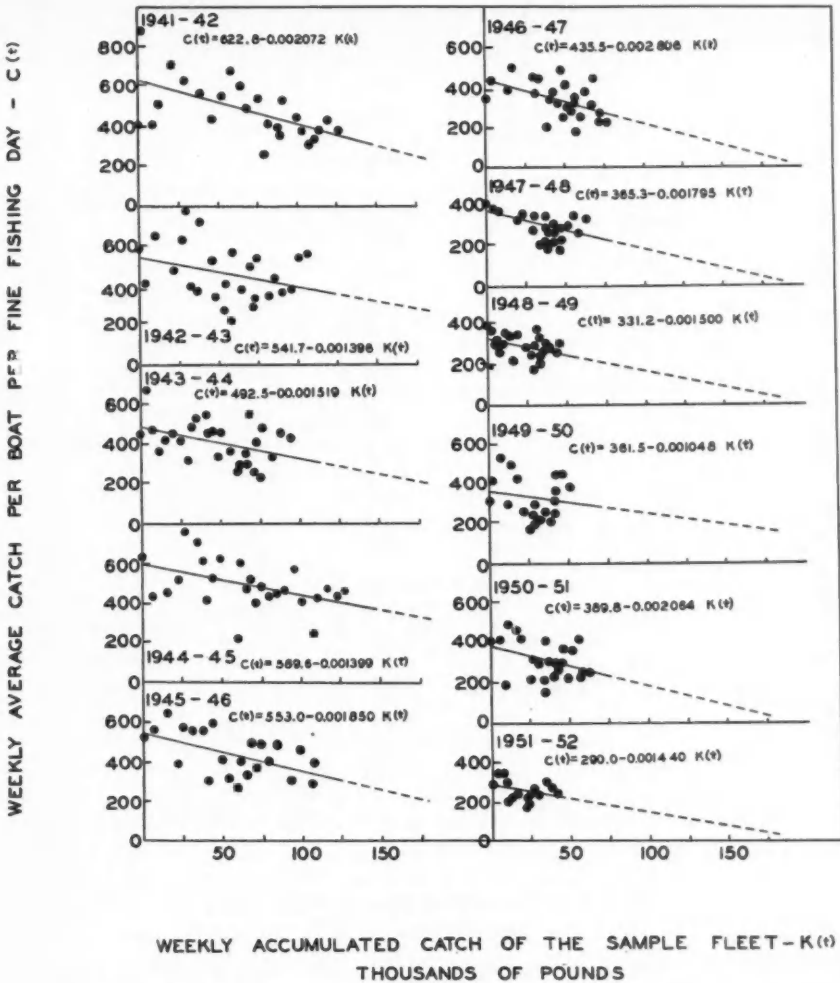


FIGURE 6. Relationship between average catch per sample fleet boat per fine fishing day in each week and accumulated catch of the sample fleet up to the beginning of that week for each season from 1941-42 to 1951-52, inclusive.

Abundance appears to have been lower, of the order of 1.6 million pounds of meats, in the next three years but dropped rapidly thereafter.

(2) Estimates of abundance based on the regression of catch per unit effort of the sample on the accumulated catch of the whole fleet are shown in Figure 4B, and the regression lines in Figure 7. Since fisheries statistics are available for

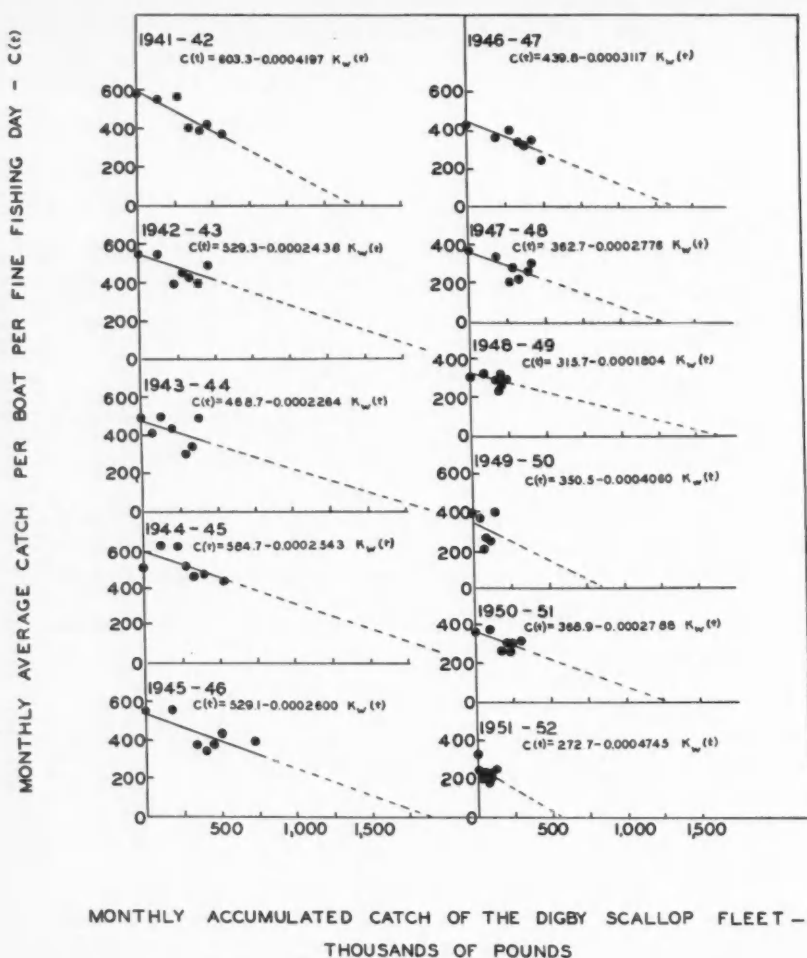


FIGURE 7. Relationship between average catch per sample fleet boat per fine fishing day in each month and the accumulated catch of the whole fleet up to the beginning of that month, for each season from 1941-42 to 1951-52, inclusive.

monthly intervals only, regression lines in these cases are based on only seven points, compared with up to 29 for each line using method (1).

According to Figure 4B the order of magnitude of the population shown by the two sets of estimates is the same, and the trend in abundance from the beginning to the end of the 11-year period is similar, although there are marked disparities between the two kinds of estimates for the 1948-49 and 1950-51 seasons.

TABLE IV. Calculations of initial abundance from catch statistics.

A. Using sample fleet statistics alone for the calculations (see equation (3) and Fig. 6):

Season	Observed regression coefficients		Correction for unsampled fleet $= 1 + \frac{k'e'}{ke}$	Correction for natural mortality $= \frac{k'e'e'}{e}$	True catchability \hat{k}	Abundance $N = \frac{kN(0)}{\hat{k}}$ (pounds)
	$kN(0)$	\hat{k}				
1941-42	622.8	.002072	5.0581	.0001527	.0003794	1,642,000
1942-43	541.7	.001396	4.8424	.0001923	.0002486	2,179,000
1943-44	492.5	.001519	4.9136	.0001967	.0002690	1,831,000
1944-45	589.6	.001399	5.3204	.0001875	.0002276	2,591,000
1945-46	553.0	.001850	7.5638	.0001929	.0002191	2,524,000
1946-47	435.5	.002086	6.7160	.0002198	.0002778	1,568,000
1947-48	365.3	.001795	6.8665	.0002362	.0002270	1,609,000
1948-49	331.2	.001510	5.8347	.0002830	.0002103	1,575,000
1949-50	361.5	.001048	3.1395	.0002643	.0002497	1,448,000
1950-51	389.8	.002064	5.3810	.0002511	.0003369	1,157,000
1951-52	290.0	.001440	3.8061	.0002913	.0003019	961,000

B. Using sample and whole fleet statistics combined (see equation (6) and Fig. 7).

Season						
1941-42	603.3	.0004197		.00003019	.0003895	1,549,000
1942-43	529.3	.0002438		.00003971	.0002041	2,593,000
1943-44	468.7	.0002264		.00004003	.0001864	2,514,000
1944-45	584.7	.0002543		.00003524	.0002191	2,669,000
1945-46	529.1	.0002600	regression is for whole fleet	.00002550	.0002345	2,256,000
1946-47	439.8	.0003117		.00003273	.0002790	1,576,000
1947-48	362.7	.0002776		.00003440	.0002432	1,491,000
1948-49	315.7	.0001804		.00004850	.0001319	2,393,000
1949-50	350.5	.0004060		.00008419	.0003218	1,089,000
1950-51	368.9	.0002788		.00004666	.0002321	1,589,000
1951-52	272.7	.0004748		.00007654	.0003983	685,000

No statistical techniques are available for establishing the confidence limits of the estimates of abundance, but their precision depends upon the reliability of the determination of the slope and position of the regression lines plotted in Figures 6 and 7. From an examination of the relative numbers of points available for each line, the scatter of the points about the lines and their spread along them, it is apparent that estimates based on the sample fleet statistics alone are the more reliable of the two sets, and in both sets the data for the first seven years are more reliable than those for the last four, where the number of points available is smaller and the scatter of points about the line is greater compared with their spread along it.

The order of magnitude of abundance, as shown by this method of calculation, may be checked against the results of a special census-fishing programme which was carried out during 1950, 1951 and 1952.

ABUNDANCE FROM CENSUS-FISHING TECHNIQUES

A programme for measuring the abundance of scallop stocks by a "strip-census-fishing" technique was begun in 1949. The method is an adaptation of the "strip-census" employed by timber cruisers in estimating potential cuts on forest plots:

1. The relative size of the scallop population was assessed by catches made in standardized hauls at regular intervals across certain of the most important scallop beds.

2. Special intensive marking experiments were carried out, to give estimates of the efficiency of the drags for taking scallops of different sizes.

3. These results were used to correct the strip-fishing catches to average numbers of scallops per square yard of bed.

4. An estimate of the size of each of the beds was made, and from these data the number of scallops present on each of the beds was calculated.

5. The relationship between meat weight and shell height was determined.

6. This relationship was used to express estimates of numbers of scallops as pounds of "meats" present on the beds, so that they could be compared with estimates from catch statistics.

STRIP-FISHING OF THE STOCKS

Trials of the strip-fishing method for estimating relative scallop population size were begun in 1949 on three of the main beds, two inshore (Buoy Ground and Broad Cove) and one offshore (Hour Ground). In 1950 a regular programme was instituted to cover most of the most heavily fished inshore and offshore areas (Fig. 2).

In strip-fishing, timed tows were made at intervals across the whole width of the selected beds. The scallop boat was run to the bed and the position of the start of the first tow determined as accurately as possible. A 15-minute tow was then made in the direction of the tide, which during full flood and ebb parallels the long straight coastline. At the end of the tow the boat was run back to the starting position, and a timed run made to one side for the starting position of the second tow. Tows were spaced at one or two minutes' run depending on the width of the bed, the variability in the density of the population as shown by variations in the catch per haul, and the time available for the census. If the bed was long, additional series were made at other points across it. This procedure was followed on the inshore fishing areas and 40-Minute Ground.

The offshore beds are large so that no exhaustive strip-fishing was feasible. However, the distribution of scallops offshore is more uniform and catches less variable than on the smaller, more irregular, rough-bottom inshore areas, so that one line of tows from one end of the most heavily fished portion to the other was considered to give an estimate of relative density of the offshore population.

As is to be expected, some of the tows were slightly shorter or longer than the standard. Furthermore some were made with a six-drag gang. The results reported in Table V are expressed in terms of catch by the more conventional seven-drag gang in a standard 15-minute tow.

A series of timed runs over a marked off course showed that a 15-minute tow covers, on the average, a distance of 900 yards. Since the width of the drag is 6 yards, each standard tow covers an area of 5,400 sq. yd. This information permits a calculation of the relative density of scallops of each size taken in the strip-fishing from year to year.

TESTS TO DETERMINE EFFICIENCY OF DRAGS

During the summers of 1949 and 1950 intensive marking programmes were carried out on small plots to determine the efficiency of scallop gear, i.e. the percentage of scallops present in their path which are actually captured by the drags. In each year a plot was marked off by buoys and living scallops were marked and placed on it. It was then sampled, a record being kept of the number and size of marked and unmarked animals recovered, and the samples replaced after each tow.

The actual performance of the experiments was beset by practical difficulties. For example, the size of the marked plot was difficult to control because the positions of the buoys marking the boundaries changed with the tide. In practice, large metal drums were anchored at the corners by $\frac{3}{4}$ -inch wire cable 100 fathoms (200 yards) long. The area was arranged with its long axis parallel to the direction of the tide and the buoys placed so that when the tide was running at full strength those at the "upstream" end were over the upper border of the bed. In this case the other buoys were some distance "downstream" from the opposite border. This is illustrated in Figure 8, which is a diagrammatic longitudinal section through the water over the marked bed used in 1949. As this diagram shows, to mark off a bed 600 yards long using buoys anchored by straight 200-yard cables, in a tide which reverses direction, the buoys should theoretically be 966 yards apart. Actually they were placed about 950 yards apart since buoy cables are catenaries rather than straight lines.

In dragging, a towing cable of about 125 fathoms (250 yards) was used. The drags were let down when the boat was abreast the upper buoys and the tow made in a line parallel to the long axis of the bed. The drags were hauled when the boat was judged to be 125 yards from the buoys at the lower end.

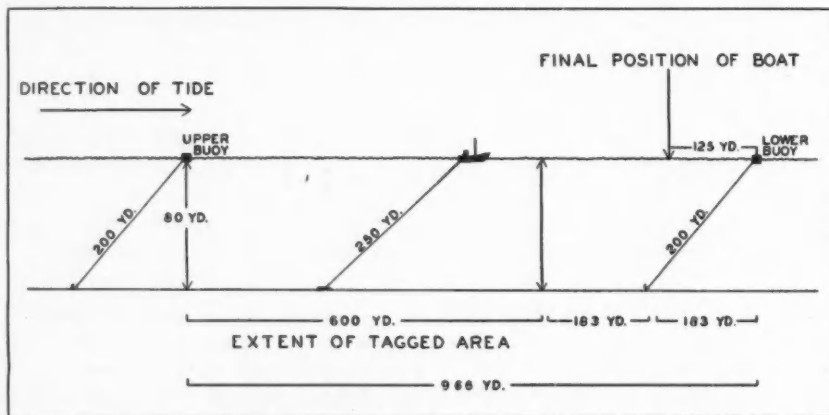


FIGURE 8. Schematic longitudinal section of the plot set out for the 1949 Buoy Ground marking experiment, showing position of buoys relative to the borders of the plot (vertical scale = $3 \times$ horizontal).

For the marked population, scallops were dragged from outside the experimental plots, marked with Volger's red ink (a carbolic acid penetrating ink) and scattered over the plot. Some of the marked animals may have drifted outside it, but a number of drags were made around it from time to time and no marked animals ever recovered in them, indicating that the number of misplaced animals must have been small.

In each of the drags made on the plot, numbers of marked and unmarked scallops were recovered. A large proportion had died as a result of the marking, so that total mark recoveries are composed of living, cluckers and single shells. The accuracy of the estimate of population present depends upon the validity of the assumption that all are equally catchable.

BUOY GROUND MARKING EXPERIMENT. Results of the 1949 marking experiment on Buoy Ground are summarized in Table VI. A total of 10,068 scallops of different sizes was marked and scattered over a plot 600 yards long and 100 yards wide. Seventeen tows were made, 13 with a gang of five commercial-mesh-size drags and four with the standard commercial gang of seven drags. A total of 1,758 scallops of different sizes was taken in these hauls, of which 381 were marked. The captures are divided into 10-mm. size-groups in the table.

The actual number of scallops of each size-group originally present on the plot may be calculated from the relationship $N/n = X/x$, where N and X are total numbers of unmarked and marked present and n and x are the numbers of unmarked and marked caught. Since the total area over which the scallops were scattered was 60,000 sq. yd., the average number of scallops of each size present per square yard of area could be determined directly.

TABLE VI. Efficiency of capture of different-sized scallops by commercial gear, estimated from marking experiment of September, 1949, on Buoy Ground. Average efficiency is calculated omitting results for 70- to 80- and 150- to 160- mm. size-classes.

Size-class (mm.)	No. marked X	Catches			Calcu- lated no. per 60,000 sq. yd. nX/x	Density =no. per sq. yd.	No. encountered per tow		No. caught per tow		Percentage efficiency	
		Un- Marked x	marked n	Total $n+x$			5 drags	7 drags	5 drags	7 drags	5 drags	7 drags
30- 40	1	0	0	0								
40- 50	7	0	1	1								
50- 60	27	0	3	3								
60- 70	58	0	1	1								
70- 80	197	1	29	30	5,713	0.095	234	342	1.8	1.3	0.8	0.4
80- 90	369	13	12	25	341	0.006	15	22	0.6	1.1	4.0	5.0
90-100	1,281	40	11	51	352	0.006	15	22	0.5	1.0	3.3	4.6
100-110	2,047	92	110	202	2,448	0.041	101	148	6.4	6.7	6.3	4.5
110-120	2,465	89	177	266	4,902	0.082	202	295	9.3	14.0	4.6	4.8
120-130	2,024	77	317	394	8,333	0.139	342	500	17.1	23.7	5.0	4.7
130-140	1,261	54	500	554	11,676	0.195	480	702	25.3	42.9	5.3	6.1
140-150	318	13	208	221	5,088	0.085	209	306	11.4	15.1	5.5	4.9
150-160	12	2	8	10	48	0.001	3	4	0.3	1.0	10.0	25.0
160-170	1	0	0	0								
Total	10,068	381	1,377	1,758		0.650	Average 4.9 ± 0.9 4.9 ± 0.5					

Each tow extended the full 600-yard length of the plot. Since the five-drag gang has a spread of 4.1 yards and the seven-drag gang a spread of 6 yards, tows by the two types of gear covered 2,460 and 3,600 sq. yd. respectively. The area towed times the number of scallops per unit area gives estimates of the average number of scallops encountered each tow. Efficiency of the gear was determined directly from the ratio of the number taken to the calculated number encountered per unit area and percentage efficiency of both types of scallop gear is shown in the last two columns of the table.

The results of this marking experiment show that the efficiency of the gear for taking the smallest, 70- to 80-mm., scallops, is very low, and for taking 150- to 160-mm. scallops is very high. But these estimates are based on recaptures of only one and two marked individuals respectively and cannot be considered as meaningful results. Estimates of efficiency of capture of size-classes from 80 to 150 mm. are based on recaptures of from 13 to 92 marks each. From these recoveries average efficiency of the five-drag gang is 4.9 ± 0.9 per cent and for the seven-drag gang 4.9 ± 0.5 per cent, or about 5 per cent each.

Estimates of scallop gear efficiency from this experiment may be presumed to apply to all inshore beds since they are similar in nature to Buoy Ground where the experiment was performed. These inshore areas are characterized by an irregular bottom on which are found many large rocks. The drags regularly bring up rocks ranging in size from a man's fist to twice the size of a head. Under such dragging conditions it is not surprising that drag-efficiency for taking small, flat scallops should be so low.

The offshore area and 40-Minute Ground are, on the average, smoother, and large rocks are uncommon, most of them being the size of a man's fist. Efficiency of scallop gear under such conditions seems likely to be higher than inshore, a difference which would explain the consistently higher catches per standard haul on offshore areas. To test this hypothesis a second intensive marking experiment was carried out on 40-Minute Ground during the summer of 1950.

40-MINUTE GROUND MARKING EXPERIMENT. Results of the 40-Minute Ground marking experiment are summarized in Table VII. A total of 9,635 scallops was marked as before and scattered over a plot 900 yards long and 75 yards wide. A total of 25 tows was made with seven-drag commercial gear to recapture them.

During the course of this experiment difficulty was experienced in keeping the tows confined to the marked plot. It was made longer than that used in 1949 so that tows would correspond more closely in length to those made by fishermen under similar circumstances. However, weather conditions confined dragging to a period of neap tides so that towing speed was reduced and cross winds often carried the boat outside the borders of the plot. This happened in 15 out of 25 tows. Of these, one was discarded and the catches of the remaining 14 adjusted to show the catch of both marked and unmarked had the tow covered the full 900-yard length on the marked plot. Of the 14, six tows were partly outside, so that only numbers of marked recoveries were adjusted in these cases. The remaining eight were shorter than 900 yards and part of the tow was outside, so

TABLE VII. Efficiency of capture of different sized scallops by commercial gear, estimated from marking experiment of September, 1950, on 40-Minute Ground. Average efficiency is calculated omitting result for the 60- to 80-mm. size-class.

Size-class (mm.)	No. marked released X	Catches			No. per 67,500 sq. yd.	Density = no. per sq. yd.	No. encoun- tered per tow	No. taken per tow	Perecn- tage effici- ency
		Marked x	Un- marked n	Total n+x					
40-50	2	0	8	8	?	.3	...
50-60	3	0	11	11	?	.5	...
60-70	50	1	111	112	5,550	0.082	443.9	4.6	1.0
70-80	445	18	682	700	16,861	0.250	1348.4	28.4	2.1
80-90	491	83	738	821	4,366	0.065	349.4	30.8	8.8
90-100	499	121	792	913	3,921	0.058	313.7	33.0	10.5
100-110	1,163	294	1,354	1,648	5,356	0.079	428.2	56.4	13.2
110-120	2,330	744	2,835	3,579	8,878	0.132	710.1	118.1	16.6
120-130	3,528	883	3,008	3,891	12,018	0.178	961.2	125.3	13.0
130-140	972	181	519	700	2,787	0.041	223.0	21.6	9.7
140-150	51	13	12	25	47	0.001	3.8	.5	13.2
150-160	1	1	0	1
Total	9,635	2,339	10,070	12,409		0.846		Average	12.2 ± 2.47

that captures of both marked and unmarked have been adjusted. A total of 1,563 marked and 8,641 unmarked were actually captured but the adjusted totals are 2,339 marked and 10,070 unmarked in 24 tows. The number of marked scallops released and the adjusted numbers of marked and unmarked captured are given in the table grouped into 10-mm. size-classes.

Efficiency of the drags on 40-Minute Ground was calculated from the ratio of numbers taken per standardized haul to calculated number encountered and is given in the last column of Table VII. The results show that only 1.6 per cent of scallops between 60 and 80 mm. present in the path of the drags are retained by the gear, but efficiency of capture of the large animals is 12.2 ± 2.5 per cent. It appears from this that efficiency of capture of large scallops is considerably higher on the smooth offshore areas than on the rough inshore areas.

EFFICIENCY OF THE DRAGS FOR CAPTURING SMALL SCALLOPS. Both marking experiments indicate that small scallops are taken less efficiently than are the larger. This is to be expected since scallops smaller than 2½ inches can escape through the meshes of the bags. Medcof (1952) has shown further that the proportion of small scallops escaping becomes higher the greater the mesh size. However, on Buoy Ground the efficiency of the drags for taking small scallops cannot be well established from the marking experiments as too few of them were recaptured. The relationship can, however, be judged from the difference in catch between a series of tows using commercial drags with the regular 2½-inch inside mesh diameter and a special drag with a mesh diameter of 1½ inches.

Catches of six Buoy Ground hauls using the two types of gear are shown in Table VIII. Six commercial-mesh drags caught an average of 103.4 scallops larger than 80 mm. per haul, while the small-mesh drags took 118, but commercial drags took only 49.5 of 70- to 80-mm. scallops while the small-mesh drag

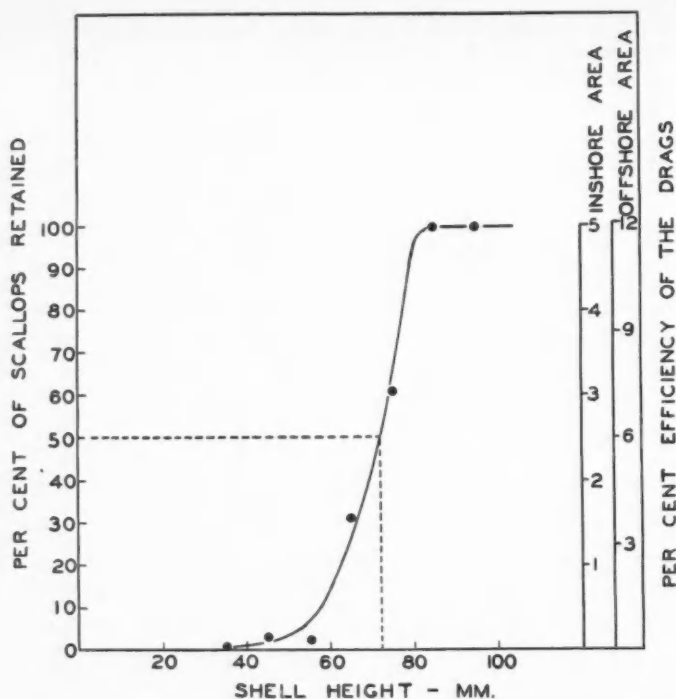


FIGURE 9. Relationship between size of scallops, the proportion of those entering drags which are retained by 2%-inch commercial mesh, and the efficiency of the drags for capturing scallops of different sizes on the rocky inshore and smoother offshore areas.

took 92. According to the marking experiments, the commercial drags take all scallops larger than 80 mm. with about equal efficiency while smaller animals escape. The small-mesh drag may be assumed to retain all scallops down to about 40 mm. shell diameter. If the commercial drag had retained small scallops as well as the small drags did, it should have taken $92 \times 102.4/118.0 = 80.6$ scallops from 70 to 80 mm. Since it captured only 49.5, it follows that commercial gear retains only $49.5/80.6 = 61.4$ per cent of this size which enter the drag. The efficiency of commercial drags for taking large scallops on Buoy Ground was 5 per cent, therefore commercial drags capture $5.0 \times 0.614 = 3.1$ per cent of 70- to 80-mm. scallops present on the beds. These calculations are given in the table, which also shows that commercial gear takes 1.6 per cent of 60- to 70-mm. scallops and only about 0.2 per cent of those between 40 and 60 mm.

These results together with the data from the marking experiments are summarized in Figure 9, and may be used to interpret the results of the strip-fishing.

TABLE VIII. Calculation of efficiency of commercial-mesh drags for taking small scallops from Buoy Ground—by comparing catches made simultaneously with commercial and special small-mesh drags. The 5 per cent efficiency of commercial mesh for capturing large scallops was estimated from marking experiments.

Size-class (mm.)	Average number scallops taken per tow with 6-drag gang		Totals > 80 mm. (at highest efficiency of commercial mesh)		Number of small scallops available to large mesh if efficient over same size range as small mesh	Small scallops retained by commercial mesh (%)	Efficiency of capture of scallops by commercial mesh (%)
	Commercial mesh	Small mesh	Commercial mesh	Small mesh			
20-30	0	0					
30-40	0	15			13.1	0	...
40-50	6.5	215			188.4	3.4	0.2
50-60	4.7	208			182.3	2.6	0.1
60-70	3.0	11			9.6	31.0	1.6
70-80	49.5	92			80.6	61.4	3.1
80-90	41.7	66					
90-100	11.5	8					
100-110	8.5	7					
110-120	28.5	20	103.4	118	...	100	5.0
120-130	10.3	15					
130-140	2.8	2					
140-150	0	0					

DENSITY OF SCALLOPS ON THE SAMPLED AREAS

Results of the drag-efficiency experiments permit calculation of the density of scallops from results shown by the strip-fishing catches as follows: From Table V the strip-fishing of Buoy Ground in 1950 captured an average of 188 scallops per standard tow. Of these, 80 had shells greater than 100 mm., 49 were between 100 and 80 mm., and 59 were less than 80 mm. Average size of scallops in each of these size-classes has been determined and was 126, 86 and 70 mm., respectively. The drag-efficiency experiments on Buoy Ground showed that scallops of over 80 mm. shell height were taken with 5 per cent efficiency. Each tow is also known to have covered 5,400 sq. yd. Therefore, one scallop greater than 80 mm. taken per standard tow on Buoy Ground represents $\frac{1}{5,400 \times 0.05} = 0.0037$ scallops per sq. yd. Similarly scallops of about 70 mm. were taken with 2.1 per cent efficiency (Fig. 9) so that one scallop of 70 mm. taken per standard haul on Buoy Ground represents $\frac{1}{5,400 \times 0.021} = 0.0088$ scallops per sq. yd. The drags took 129 scallops greater than 80 mm. and 59 of about 70 mm., therefore the density of catchable scallops present on Buoy Ground in 1950 = $(129 \times 0.0037) + (59 \times 0.0088) = 0.997$ per sq. yd. Similarly the density of scallops on Buoy Ground in 1951 was $(284 \times 0.0037) + (175 \times 0.0088) = 2.591$ per sq. yd.

The density of scallops on all surveyed inshore areas was calculated in this way and the results are shown in Table IX. A similar method was used for 40-Minute Ground and Hour Ground, using the drag-efficiency estimates of 40-Minute Ground to correct the strip-fishing catches. Results of these calculations are also shown in Table IX.

TABLE IX. Calculations of abundance of scallop stocks from the results of the strip-census fishing.

1	2	3				4			
Scallop bed	Area in sq. yd.	Number of scallops per square yard				Population of the bed in thousands			
		1950	1951	1952	1953	1950	1951	1952	1953
Inshore:									
Buoy Ground	1,560,000	.9965	2.5908	3.5020	3.4364	1,555	4,042	5,463	5,361
Broad Cove	1,620,000	.6539	1.3144	1.8533	1.4904	1,059	2,129	3,002	2,414
Gulliver's Cove	1,620,000	.9117	4.1071	1,477	6,654
Shelburne Cove (First Ridge)	2,430,000	1.2863	3,126
Shelburne Cove (Second Ridge)	1,620,000	.7773	(1.0744) ^a	1.3715	7.6187	1,259	(1,741) ^a	2,222	12,342
Centreville	1,620,000	1.1767	3.8230	1,906	6,193
Intermediate:									
40-Minute Ground	3,780,000	.4858	.7316	.7829	1.0253	1,836	2,765	2,959	3,876
Offshore:									
Hour Ground	31,500,000	1.6929	1.2662	1.0237	1.1123	53,326	39,885	32,247	35,038
		5				6			
		Average weight of a scallop, in pounds				Population of the bed, in thousands of pounds			
		1950	1951	1952	1953	1950	1951	1952	1953
Inshore:									
Buoy Ground	.0313	.0263	.0230	.0266		48.7	106.3	125.7	142.6
Broad Cove	.0467	.0393	.0314	.0329		49.5	83.7	94.3	79.4
Gulliver's Cove	.03980256		58.8	(96.0) ^c	(133.2) ^c	170.3
Shelburne Cove (First Ridge)	.0319		99.7	(162.8) ^d	(225.8) ^d	(288.7) ^d
Shelburne Cove (Second Ridge)	.0365	(.0373) ^a	.0380	.0199		46.0	(64.9) ^a	84.4	245.6
Centreville	.03450242		65.8	(92.8) ^b	(120.7) ^b	149.9
Intermediate:									
40-Minute Ground	.0256	.0244	.0252	.0239		47.0	67.5	74.6	92.6
Offshore:									
Hour Ground	.0208	.0210	.0213	.0207		1,109.2	837.6	686.9	725.3
Population totals in thousands of pounds									

TABLE X. Dimensions of the principal Digby scallop beds.

Name of bed	Surveyed area			Total area	
	Length	Width	Area	Size relative to surveyed area and direction of its extension	Dimensions sq. yd.
Buoy Ground	<i>yards</i> 1,300	<i>yards</i> 600	<i>yd.²</i> 780,000	2 × surveyed, extending to westward	10 ² <i>yd.²</i> 1,560
Broad Cove	900	900	810,000	2 × surveyed, to west and north	1,620
Shelburne Cove, First Ridge	900	900	810,000	3 × surveyed, to east and west	2,430
Shelburne Cove, Second Ridge	900	600	540,000	3 × surveyed, to east and west	1,620
Centreville (Inshore)	900	1,200	1,080,000	1½ × surveyed, to north	1,620
40-Minute Ground	1,800	1,400	2,520,000	1½ × surveyed, to east	3,780
Hour Ground	5,000	3,150	15,750,000	2 × surveyed, to east and west	31,500

series of strips on Buoy Ground covered the main fishing area. Each tow was about 650 yards long and the inside and outside edge tows about 600 yards apart. The total sampled area was then 780,000 sq. yd. However, fishermen estimate that there is an additional profitable dragging area about the same size as the surveyed area but to the west of it. Therefore, $2 \times 780,000 = 1,560,000$ sq. yd. have been taken as the total area of Buoy Ground.

The dimensions of that part of each bed sampled during the 1950 "exploratory" dragging and strip-fishing and the estimated size of the whole of each scallop bed are shown in the table. The sizes and positions of these have been checked by several scallop skippers.⁴

From the density of catchable scallops present on each bed in each year, and the total area of each bed, estimates have been made of the total "catchable" population. This is entered in column 4 of Table IX.

These estimates of numerical strength of the scallop population may be converted to weight of scallop meats for comparison with abundance estimates based on catch statistics.

RELATIONSHIP BETWEEN SHELL HEIGHT AND MEAT WEIGHT

The relationship between the diameter of the shell (shell height) and the meat yield of scallops has been determined. Figure 10A shows this relationship for scallops from Buoy Ground, and is based on a series of 86 measurements made in September, 1948, by Medcof (1949), and on an additional series of 80 measurements made by the writer in September, 1950. The curve is fitted to the points by inspection. Figure 10B shows a similar curve for the Shelburne Cove area based on unpublished data collected by Medcof in September, 1948, and Figure 10C the curve for Hour Ground based on measurements made by Medcof and MacPhail in September, 1948, and by the writer in July, 1949. The Buoy Ground measurements are considered to represent scallops from Broad Cove and Gulliver's Cove as well. Shelburne Cove data have been applied to the Centre-

⁴The writer particularly depended on the assistance and advice of Messrs. Lewis Hudson, Jesse Magarvey, and Robert Longmire in determining the position and size of the scallop beds.

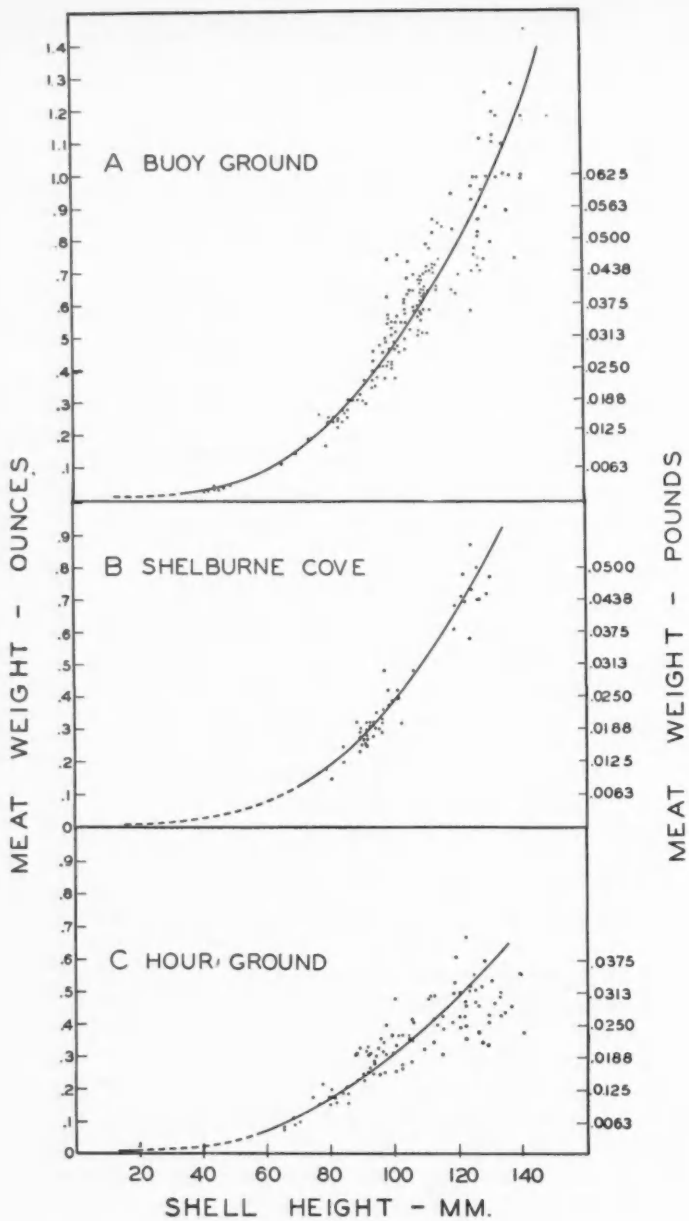


FIGURE 10. Relationship between meat weight and shell height in Digby scallops.

ville area. The 40-Minute Ground scallops do not have as high a meat yield as inshore scallops, and although they are not as small as Hour Ground scallops, they are more like them than like inshore scallops. For present purposes the Hour Ground measurements are assumed to be typical of scallops from both the Hour Ground and 40-Minute Ground.

ABUNDANCE BY WEIGHT FROM STRIP-FISHING CATCHES

The relationship between shell height and meat weight was used to convert numerical abundance of scallops to abundance by weight as is illustrated by the following example: The 1950 strip-fishing of Buoy Ground showed 59, 49 and 80 scallops having an average shell size of 70, 86 and 126 mm. respectively. Scallops of these sizes have meats weighing 0.0094, 0.0181 and 0.0556 lb. each. Average weight of scallops on Buoy Ground in 1950 was therefore:

$$\frac{(80 \times 0.0556) + (49 \times 0.0181) + (59 \times 0.0094)}{188} = 0.0313 \text{ lb.}$$

This is entered in column 5 of Table IX, as is average weight of scallops on each other bed in each year. Abundance of scallops by weight is then total number times average weight, which in 1950 on Buoy Ground was $1,555 \times 0.0313 = 48.7$ thousand pounds. Abundance by weight of scallops, on each of the beds is given in column 6, Table IX.

The data of column 6 indicate that during the summer of 1950 there was a total of about 1.525 million pounds of scallop meats present on the principal Digby scallop beds. Of this total, over 1.109 million pounds were present on Hour Ground alone, the remaining 0.416 million being distributed among the inshore and 40-Minute Ground areas. During the subsequent two years the total stocks appear to have remained almost constant, increasing slightly in 1953. This relatively steady total population has, however, been accompanied by marked changes among the beds. In three years the inshore population, which has always been the mainstay of the winter fishery, has increased rapidly—threefold on Buoy Ground, double on Broad Cove and fourfold on Shelburne Cove Second Ridge and presumably by comparable amounts on the other western beds. The 40-Minute Ground population increased slightly in this time and the offshore population decreased. By 1953 the inshore beds and 40-Minute Ground supported 0.858 million pounds or 55 per cent of the total in contrast to only 27 per cent in 1950. These data have been plotted in Figure 4C.

The estimates of abundance based on the strip-census-fishing technique are subject to errors which are difficult to detect, and the importance of which is hard to assess. Most liable to such errors are the estimates of density of scallops given in column 3, based as they are on the indirect evidence of catches with inefficient scallop gear and the results of marking experiments to determine gear efficiency. For this reason underwater photography was employed to check them.

The only other potentially large source of error in the strip-fishing method is in the estimation of the area of each of the beds. In the writer's opinion, this

error is not great and in any case such errors bias results in every year equally and do not effect comparisons of changes in abundance from year to year.

CHECKS OF ABUNDANCE ESTIMATES BY SUBMARINE PHOTOGRAPHY

Two underwater photographic surveys were made, one during the summer of 1950 and another in 1952, to determine the density of the scallop population of some of the areas sampled in the strip-fishing and drag-efficiency experiments. The apparatus used is described in detail by Ewing, Vine and Worzel (1946) and was built at the Woods Hole Oceanographic Institute.

A systematic census of the scallop beds, like that described by Vevers (1951), was found to be impossible because of technical difficulties with the operation of the photographic apparatus. The adverse effects of the deep water over the beds (40-60 fathoms), strong tides, and apparent irregularities in the transparency of the turbid bottom water caused many misfires, exposure failures and fogged or blurred negatives. Despite these difficulties, however, a number of satisfactory pictures was obtained.

In September, 1950, a total of 97 exposures were made on and immediately surrounding the 40-Minute Ground marked area. Of these, 27 were blurred, fogged or out of focus too badly to be useful for identifying objects on the bottom. Of the remainder, 53 permitted reliable identification of scallops larger than about three inches in shell diameter. A further 17 were clear photographs comparing favourably with those published. In May, 1952, 221 exposures were made on Hour Ground and on Shelburne Cove Second Ridge. Thirty-six reliable prints were obtained and another 78 permitted positive identification of scallops larger than about three inches in shell diameter. The remainder were too badly blurred or fogged to permit interpretation.

The average density of scallops was determined directly from the average number shown in the successful exposures. The area represented by each negative was calculated from the known size of the reflector and its apparent size in each photograph, from photographs of a calibrated stick affixed to the bottom of the pole and from camera-to-bottom and reflector-to-bottom distances. An area of 1.5 sq. yd. was included in each negative with a camera-to-bottom distance of nine feet, and 1.4 and 1.6 sq. yd. with camera-to-bottom distances of 8 and 10 feet, respectively.

Numbers of successful exposures per roll of film, total area photographed, numbers of scallops detected and scallop population density are given in Table XI. The photographs on 40-Minute Ground showed an average population density of 0.52 ± 0.24 scallops per sq. yd. In this survey only 17 photographs were clear enough to permit positive identification of small scallops. Fifty-three were so blurred that scallops of less than about 80 mm. shell diameter might be confused with other objects. Therefore densities have been determined for only that part of the population of greater than about 80 mm. From the marking experiment carried out on 40-Minute Ground at the same time, the density of scallops larger than 60 mm. was 0.85 per sq. yd. Of this total catchable population, the density of that part of it greater than 80 mm. was 0.55 per sq. yd.

TABLE XI. Calculations of scallop population density as shown by submarine photography.

Date	Roll No.	Number readable exposures	Area photographed	Number scallops	Density	Average density	Standard error of density
			sq. yd.		no./sq. yd.	no./sq. yd.	no./sq. yd.
1950—40-Minute Ground							
Aug. 12	1	4	6	8	1.33		
	2	1	1.5	1	.67		
Aug. 25	1	6	9	2	.22		
Sept. 18	1	18	27	12	.44	0.52	± 0.24
	2	10	15	5	.33		
Sept. 22	1	12	18	9	.50		
	2	32	48	24	.50		
	3	13	19.5	9	.46		
Sept. 26	1	13	19.5	13	.67		
Total		109	163.5	83			
1952—Hour Ground							
May 7	1	4	6.4	6	.94		
	2	4	6.0	4	.67		
	3	5	7.5	6	.80		
May 9	4	4	6.0	5	.83		
	5	9	13.5	8	.59		
	6	13	19.5	17	.87	0.72	± 0.14
	7	6	9.0	8	.89		
May 10	9	7	10.5	7	.67		
	10	11	16.5	13	.79		
May 11	11	6	9.0	5	.56		
	12	6	9.0	4	.44		
	12a	9	13.5	4	.30		
May 13	16	7	10.5	12	1.14		
Total		91	136.9	99			
1952—Shelburne Cove (Second Ridge)							
May 13	13	9	13.5	9	.67		
	14	6	9.0	9	1.00	0.81	± 0.41
	15	8	12.0	10	.83		
Total		23	34.5	28			

The 1952 Hour Ground photographic survey showed an average density of scallops larger than 80 mm. of 0.72 ± 0.14 per sq. yd. The combined drag-efficiency experiments and 1952 strip-fishing data indicate a density of these sizes of 0.90 per sq. yd. The photographic survey of Shelburne Cove Second Ridge in 1952 showed 0.81 ± 0.41 scallops larger than 80 mm. per sq. yd. compared with the strip-census result of 1.25.

The close agreement between estimates of density of scallops on 40-Minute Ground from the drag-efficiency experiments and from the photographic survey conducted there at the same time suggest that the methods may be relied upon to give an accurate estimate of the density of scallops present on that bed. But the tendency for the strip-census estimates on Hour Ground and Shelburne Cove to exceed the photographic survey figure suggests that the efficiency of the drags on these areas may be slightly higher than it was on the key areas with which they were compared (40-Minute Ground and Buoy Ground, respectively). This result might have been expected from a knowledge of the nature of the beds, since both appear to be smoother and less rocky than the

key areas. The disparities are, however, not great and indicate that strip-census estimates of abundance are of the right order of magnitude.

ABUNDANCE ESTIMATES FROM COMMERCIAL RETURNS OF MARKED SCALLOPS

In addition to the above methods of estimating abundance the results of one preliminary marking experiment are available. The estimate based on commercial returns of these marked scallops, although of limited value by itself, may be used as a rough check on other methods. In September, 1947, scallops were marked with Volger's red ink and released by Dr. J. C. Medcof, of the Atlantic Biological Station, assisted by Mr. J. S. MacPhail. Rewards were offered for these and a large proportion of them was returned. Results of the experiment are summarized as follows:

Area:		Buoy Ground	Shelburne Cove area
No. released:	Sept., 1947	150	1,000
Recoveries:	Oct., 1947	47	2
	Feb., 1948	1	18
	Apr., 1948	—	103
Total:		48	123
Percentage recovery		32	12.3

It is of some importance that recoveries during the first month of the season were high from Buoy Ground, an area close to harbour (Fig. 2), but low from the more distant Shelburne Cove area, and that this situation was reversed towards the end of the season. This shift is indicative of some systematic exploitation of the beds, and suggests that, other things being equal, the beds nearest harbour will be exploited first and most heavily. However, it is known that in some years, for example 1950-51 and the beginning of 1953-54 and 1954-55, this was not the case, and from discussions with scallop fishermen it appears that, in general, the order in which the beds are fished is determined by the relative size of the catch to be made from them, although beds closest to harbour are fished most heavily. This is an important consideration in interpreting the estimates of abundance based on sampling and removal data, and relative abundance estimates.

It is difficult to interpret the returns for making abundance estimates because many returns were of single shells or intact empty shells, indicating high mortalities despite precautions taken to avoid them, and there is no assurance that drags capture living scallops and empty shells equally efficiently. Furthermore, during drag-efficiency experiments, the writer found that fishermen, accustomed for years to sorting scallops from the debris of the catch as quickly as possible, miss the marks on empty and single shells unless special precautions are taken to sort all shells very carefully. In addition to this, in the monotonous, mechanical, but extremely rapid shucking process, many fishermen will shuck out a meat and throw the shell overboard before they realize it was marked. Therefore, the ratio of living to dead marked scallops actually caught and that

returned is likely to be different, and returns of empties are likely to be low relative to the returns of shells from living scallops. Interpretation of returns is made more difficult because it is not known how much fishing was done on different areas, or how much of the total catch came from the populations into which marked animals had been introduced. All these factors tend to make estimates of population size from marked scallop returns too large. However, calculations may be made and the results regarded in this light.

According to monthly Fisheries Statistics collected by the Department of Fisheries (F.S.I's) a total of 449 thousand pounds of scallops was landed at Digby in 1947-48. Of this total, 342 thousand pounds were caught from October to February inclusive, and 107 thousand in March and April. If it is assumed that the rate of exploitation during the first period of capture was similar to that of Buoy Ground then:

$$\frac{342}{N} = \frac{48}{150}$$

from which $N = 342/0.32 = 1.069$ million pounds. Similarly if the remaining catch was taken at the same rate as that from Shelburne Cove:

$$\frac{107}{N} = \frac{123}{1,000}$$

whence $N = 107/0.123 = 0.870$ million pounds. Total population from which the catch was taken is the sum of these, or approximately 1.9 million pounds.

This population "estimate" of 1.9 million pounds is almost certainly too large, but may be compared with the 1947 population estimate made from the sampling-removal data in Figure 4B—1.6 million pounds. The fact that this estimate is lower than the estimate from the marked scallop returns is support for the conclusion that abundance estimates based on the sampling-removal data are of the right order of magnitude.

DISCUSSION OF ABUNDANCE ESTIMATES

The estimates of abundance from catch statistics and special techniques have been plotted together in Figures 4A to 4C and may be compared.

For 1941-42 Figure 4A gives two estimates of relative abundance based on average catch per unit effort for the whole and sample fleets respectively. They indicate a high abundance that year relative to other years. But the estimates in Figure 4B based on sampling and removal data indicate that abundance for 1941-42 was lower than average. This discrepancy may have resulted from an unusual price change that took place that year, and which would be likely to have influenced each abundance estimate in a different way.

Fisheries Statistics of Canada show that previous to 1941 the market price of scallops was low, ranging from 12 to 20 cents per pound, with an average of 16.5 cents in the ten-year period 1931 to 1940. But in 1941 and 1942 price rose to 22 and 34 cents, respectively, and has remained high since. Statistics of the United States fishery show a similar rise in price. These reports are averages for the calendar year, but the 1941-42 scallop fishing season has three months in

1941 and four in 1942, overlapping the statistical reports, so that the full effect of the price rise of 1941 and 1942 came into effect during the 1941-42 season. It seems likely that the rise in price to nearly twice its previous level may well have influenced fishermen to fish harder. This conclusion is supported by the fact that the sample boats fished an unusually large number of days during that season compared with the remainder of the study period (80 compared with the next highest of 65 days in 1944-45, and an average for the 11-year period of only 56, see the Appendix).

When extra effort is being put forth by each boat, catch per boat per day during the first part of the season would be expected to be higher than usual, relative to the population present. Seasonal average catch would be lower than initial catch, but may still be high relative to the same population in more normal years, depending on how large a proportion of the total population was caught. But seasonal rate of decrease in catch per unit effort will always depend simply upon the proportion of the original stock removed by the fishing effort, so that the sampling-removal data should give an accurate estimate of initial abundance whether effort is high or low, so long as catchability does not change appreciably during the season. In 1941-42 daily catch per boat at the first of the season was 22 per cent above average for the 11-year period, seasonal catch per boat was 13 per cent above average, but actual abundance was 8 per cent below average. On the assumption that catchability was constant, it may be concluded that 1941-42 estimates of relative abundance were falsely high because price induced greater effort, but that the actual abundance of the population was less than the average for the 11-year period, and is more accurately estimated from Figure 4B.

From 1942-43 to 1949-50 the trends in estimates of relative and actual abundance correspond closely, but there is consistently closer agreement between estimates from seasonal catch in Figure 4A and those based on the sample fleet data (correlation coefficient 0.975) in Figure 4B than between the latter and initial seasonal catch in Figure 4A (correlation coefficient 0.792), despite the fact that the second comparison is based entirely on sample fleet statistics, while seasonal catch in the first comparison is taken from Fisheries Statistics. The explanation for this appears to lie in the fact that the relative abundance estimates in the second comparison are based on catches made only at the start of the season by a sample fleet which formed a variable proportion of the whole fleet from year to year. The index may therefore suffer from special conditions which hold only at the start of any particular season. For example, it may be unduly influenced by the catch from one particular bed (see the 1947 marking experiments, p. 834) or by variations in catch which take place while boats are exploring the beds and trying out new fishing gear or new crews. By contrast, the close agreement in the first comparison, both estimates using the entire season's catch, suggests that catches for the whole season must be used if valid estimates of average abundance for the whole fished area are to be obtained.

In 1950-51 and 1951-52 there is again a considerable difference between the trend of relative abundance and actual abundance estimates. It has been

pointed out above (p. 819) that both of the Figure 4B estimates are not as reliable for more recent years as they are for the earlier period, and discrepancies may result in part from large sampling errors. However, this difference is explicable on the basis of a known change in fishing area and the nature of this change is of sufficient importance to warrant closer examination of the estimates for these two years.

Fishermen estimate that in "normal" years 70 to 90 per cent of the total catch comes from the inshore beds, so that estimates of abundance for the major part of the study period apply principally to the inshore areas. However, beginning in 1945-46 there was a marked decrease in inshore abundance. At first the fleet continued to fish the inshore beds at the beginning of each season, moving to the less familiar offshore areas only when it became apparent that profitable catches could not be made otherwise. But in the summer of 1950, the offshore areas were opened to a summer fishery. The result was an increase in fleet size and thorough exploration of the offshore areas, so that when the 1950-51 winter season began the boats continued to fish exclusively offshore. Extensive offshore fishing continued in 1951-52, although towards the latter part of that season it is known that some fishing resumed inshore. It appears, therefore, that abundance estimates which in former years had largely represented inshore areas, in 1950-51 and 1951-52 represented principally the offshore areas, a distinct change in the average population fished.

It was shown above that the efficiency of scallop gear for offshore fishing is over twice that for inshore (12.6 per cent compared with 5.0 per cent). Therefore, offshore catch per boat per day from 1950 to 1952, which is the basis for relative abundance estimates, will be higher than it would be for the same population inshore, although the difference is not as great as indicated by drag-efficiency alone because offshore meat weight per scallop is less, and scallops are smaller, than inshore. On the other hand, abundance estimates based on sampling and removal data will still depend simply on the proportion of the total fished population removed, whether inshore or offshore populations are fished. It is to be expected, then, that if the fleet shifts from combined inshore and offshore to exclusively offshore fishing, actual abundance of the fished population will be lower than usual, but average catch per unit effort will be higher. The difference in efficiency of fishing on the two areas appears, therefore, to account for the disagreement between the abundance estimates from 1950 to 1952.

This explanation for the change in the relationship between relative and actual abundance estimates in 1950-51 and 1951-52 may be checked by comparing the latter with estimates of abundance based on the strip-fishing experiments (Figure 4C). They show that total population present in the Digby area in 1950 was of the order of 1.525 million pounds (Table II), but that the offshore population was 1.109 million pounds of this. The best 1950 estimate of abundance of the fished population in Figure 4B is 1.230 million pounds, which corresponds closely with this offshore population. Similarly in 1951 the strip-fishing showed a total population of about 1.512 million pounds of which 0.838 million were offshore scallops. The total fished population for that year was

0.969 million pounds. From the close agreement between these estimates of offshore and total fished population it can only be concluded that the discrepancy among abundance estimates for 1950 and 1951 has resulted largely from the change from combined inshore and offshore to exclusively offshore fishing. That is, relative abundance appeared to be higher than previously because of greater efficiency of offshore dragging, but actual abundance was lower because the fishery was exploiting only that part of the population present on the offshore areas.

On the basis of the foregoing comparisons, and particularly because of the close agreement between the 1950-51 and 1951-52 estimates of abundance derived from the independent strip-census fishing (Fig. 4C) and detailed sampling-removal data (Fig. 4B), the conclusion that the two sets of data show the correct order of magnitude of the scallop population seems fully justified. It further appears from the same comparisons that both methods of estimating abundance are sensitive enough to detect changes in the population fished with a fair degree of accuracy. From Figure 4B it must be concluded, then, that during the period 1941-42 to 1951-52, there have been fluctuations in the abundance of the stocks fished on the Digby scallop beds. Abundance appears to have risen from about 1.6 million pounds in 1941 to a high of from 2.6 to 2.5 million pounds in 1944 and 1945, then in 1946 to have dropped to about 1.6 million pounds, a level which it has maintained from then until about 1952. However, during this period of relatively stable total abundance there have been continued changes in the constitution of the population of the beds. The early years of fishing were confined principally to the inshore areas which supplied at least 70 to 75 per cent of the total catch, so the rise in 1944 and the drop in 1946 mainly represent changes in the abundance of the inshore population. During more recent years this inshore population was reduced to such a low level that in 1950-51 fishing was confined to the offshore area. Detailed data from strip-fishing of the stocks indicate that in 1950 the inshore population was only about 30 per cent of the total. By 1950, however, the trend toward decreased inshore abundance had been reversed, and in 1953 it was more than double its 1950 level, and made up over 50 per cent of the total stocks. In 1952-53 the fishing was again confined to the inshore areas, on which the population has continued to increase.

These conclusions are based on the sampling-removal data which are available for the 11-year period beginning in 1941. Previous to this the only measure of abundance changes is relative abundance based on seasonal catch per boat—Figure 4A. But the above analysis has also shown that throughout the 11-year period this relative abundance estimate corresponds closely with actual abundance with three exceptions which were indicative of special circumstances. Barring similar exceptional circumstances previous to 1941, seasonal catch per boat may be used to show abundance changes back to about 1936. Previous to 1936 it is known that changes in methods of fishing were taking place and no reasonably accurate estimates of relative abundance can be obtained.

With this information on changes in the total abundance of the scallop

stocks, it remains to examine the nature of the changes in more detail, and to discover the factors that have been responsible for them.

CAUSES FOR CHANGES IN ABUNDANCE

The now classic work of Hjort and his co-workers was the first to clearly demonstrate the importance of changes in year-class strength in producing fluctuations of landings of fish. They showed that a single, exceedingly strong year-class of herring may dominate the Norwegian herring fishery for several years, resulting in an abundant fishing stock and high catches, while a succession of poor broods led to low abundance and poor catches. Similar phenomena have been demonstrated in connection with studies of fluctuations of other species of fish as well as for a number of species of marine littoral and benthic invertebrates and were noted in the introduction of this paper. These studies also showed that such fluctuations result largely from the effects of hydrographic conditions on the survival of early, vulnerable stages in the life-history of the animals. The same appears to be true for scallops in the Bay of Fundy.

SIZE- AND AGE-COMPOSITION OF CATCHES IN GOOD AND POOR FISHING SEASONS

Samples of the scallop stocks have been taken from time to time since 1937 and show the size-composition of the stocks in both good and poor fishing seasons. Two series of such records are presented in Figure 11. Series A shows changes in the percentage size-composition of a series of samples of the stocks on inshore beds from 1937 to 1940, a period of rapidly decreasing abundance after the peak year in 1936-37 and just previous to a slight increase in abundance in 1941. Samples were taken annually at several inshore stations from 1937 to April, 1940, by Captain A. E. Calder of the Atlantic Biological Station, using a special small-mesh drag. The November, 1940, measurements were made of shells of those scallops caught and landed by commercial fishermen.

Comparison of the series A histograms with abundance as estimated from average seasonal catch per boat (Fig. 1B) shows that as catches declined from 1936 to the low between 1938 and 1940, the catches, which were at first dominated by scallops ranging in size from 115 to 125 mm., gradually came to consist of relatively fewer large scallops. At the same time a number of smaller scallops were appearing in the population and were captured by the special small-mesh sampling gear. But commercial gear in use from 1933 to 1952 allowed a proportion of all scallops smaller than 80 mm. which entered the drags to escape again, with 50 per cent retention at about 73 mm. (Fig. 9); so these small scallops did not contribute appreciably to commercial catches until 1939.

In 1939 the year to year reduction in landings ceased, and in 1940 and 1941 they increased slightly.

Series B shows the size-composition of inshore catches taken with commercial gear during the summers of 1948 to 1952. Previous to 1948, abundance was rapidly decreasing after a maximum in 1944 and 1945. The first histogram of series B represents the stock remaining in 1948. Two size-groups are clearly distinguishable, with modes at 105 to 110 and 135 to 140 mm. Throughout 1948,

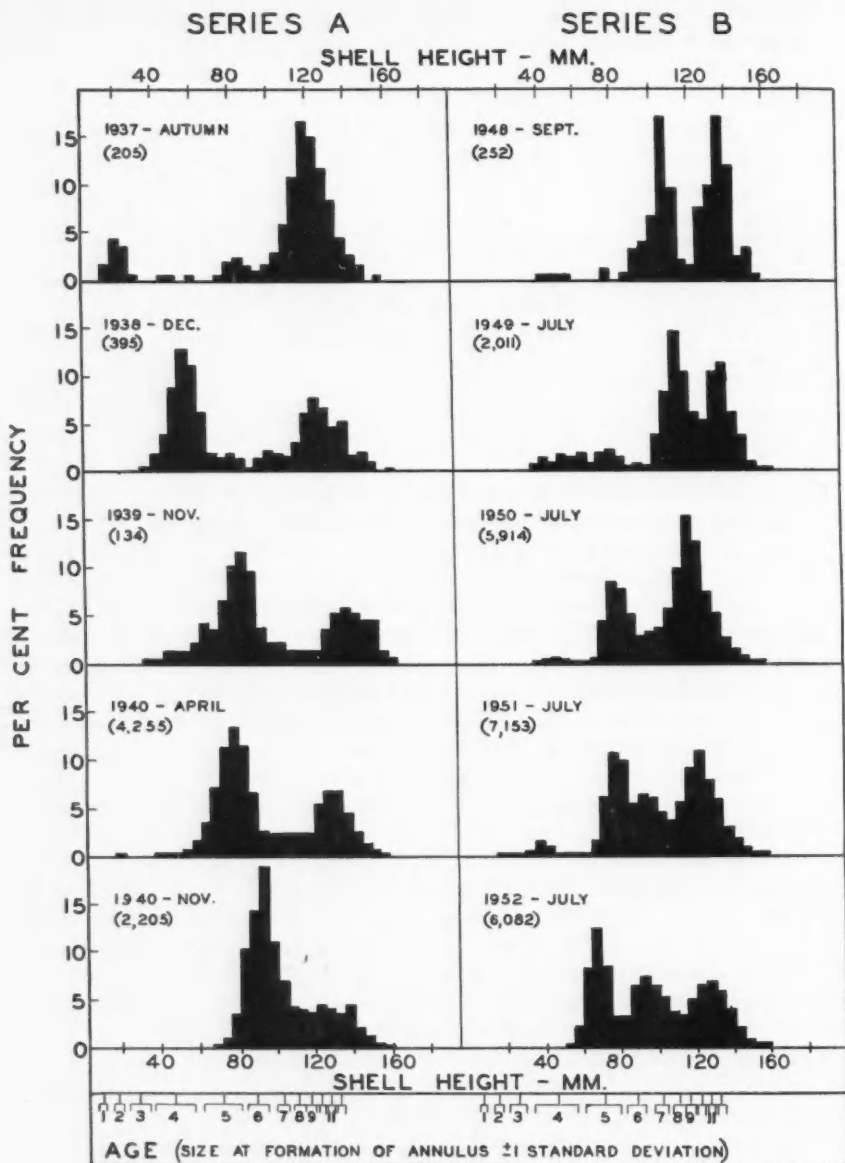


FIGURE 11. Percentage size-frequency distribution of catches of scallops from inshore beds off Digby, N.S. Numbers in brackets under the date show the number of scallops measured in each sample. Samples from 1937 to April, 1940, inclusive, were taken with small-mesh drags; the remainder were taken with commercial-mesh (2" inside diameter of the rings).

1949 and 1950 it is apparent that the fishery continued to be dependent upon the stocks of large animals, and abundance remained low. However, by 1950 small scallops entered the commercial catches and during the next two years formed an increasingly important part of it. At the same time, the strip-census records of Figure 4C show that on the inshore beds the downward trend in abundance of catchable stocks was reversed and abundance increased appreciably through 1952, although total catches were still low and total stocks almost constant from 1950 to 1952, inclusive.

These two series of size-composition data together with the abundance indices show that when the stocks are composed for a number of seasons of large scallops alone, abundance becomes progressively lower, due undoubtedly to the excess of removals of scallops by fishing and natural mortality over growth. But as new size-classes are recruited, abundance increases, at first slowly because the meat yield and efficiency of capture of small scallops is low, then rapidly as with growth they become heavier and fully enter the catchable population.

There can be little doubt that the distinctive size-classes in these samples of the scallop population, represent age-classes which appear in the population, grow to catchable sizes over a period of years to merge gradually with the larger sized stocks and diminish in numbers as they are fished and die from natural causes. This supposition is confirmed by studies of the growth rate of Digby scallops reported by Stevenson and Dickie (1954). The data from their growth curve have been used to add an age abscissa to Figure 11 and it may be used to identify the modes in the percentage size-composition polygons according to year-classes.

In series A, the 1937 sample shows modes in the size-distribution from 15 to 20 mm., 80 to 85 mm. and 115 to 120 mm. Since these scallops were collected in late fall, and Digby scallops deposit the growth ring during the winter (Stevenson and Dickie), then during the winter of 1937-38 the scallops represented by these modes would have formed the third, sixth and eighth to tenth annuli respectively. They were, therefore, 2-, 5- and 7- to 9-year-olds, and belonged to the 1935, 1932 and 1928 to 1930 year-classes.

In the remaining samples of series A, taken from 1938 to 1940, the first mode may again be identified as the 1935 year-class. It dominated the small-mesh samples of 1938 in which it appeared to be about equal in numerical strength to the weak commercially catchable stock of 1938. It grew large enough to enter the commercial catches of 1939-40, and by the beginning of the 1940-41 season was the mainstay of the fishery. The 1932 year-class had become merged with the 1928 to 1930 year-classes by 1939 and the number of these larger animals became progressively diminished from year to year and was low by 1940-41.

The first polygon of series B represents a sample of scallops taken in September, 1948, and shows three distinct modes at 40 to 60, 105 to 115 and 130 to 145 mm. Comparison of the size-modes with the age abscissa shows that the year-classes in this sample represent animals which would already have deposited

their 4th, 8th or 9th and 10th or later annuli, and belonged, therefore, to the 1944, 1940 or 1939 and 1938 or older year-classes.

The remaining polygons of series B represent samples taken from the in-shore beds during July of each summer, by which time scallops have completed the annual winter ring and realized about one-third of their annual growth (Fig. 12). In the 1949 samples, modes at 40 to 60 and 70 to 80 mm. are therefore four- and five-year-olds or the 1945 and 1944 year-classes, respectively, while modes at 110 to 115 and 130 to 140 mm. represent remnants of the 9 or 10 and 11 or older ages, that is, the 1940 or 1939, 1938 and older year-classes.

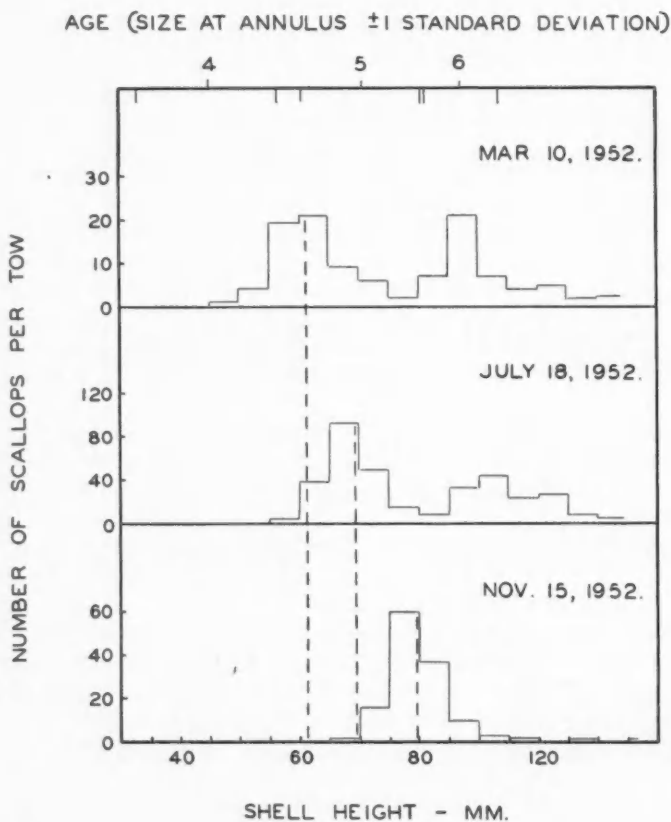


FIGURE 12. Seasonal growth shown by the average size (dashed lines) of a size-class in samples taken from Buoy Ground at different times during 1952. The annual growth ring is deposited in March, and the scallops represented by the left mode would deposit their 5th. Since expected annual increase of 5-year-olds is 22.5 mm., by July average growth was 36 and by November was 85 per cent of the expected annual. (Size-composition data for March and November kindly supplied by Dr. J. C. Medcof and Mr. J. S. MacPhail.)

The 1950 samples are the first of series B to show a prominent mode as small as 60 to 80 mm., representing the 1945 year-class. Also present were a few scallops representing the 1946 year-class and the 1939 or 1940 year-classes. The 1938 and older year-classes had largely disappeared.

The 1951 and 1952 samples indicate growth of the 1945 year-class which became progressively reduced in importance while the 1946 and 1947 year-classes appear in the commercial catches first as only partially catchable five-year-olds, but fully catchable by the time they were 6 years old.

Since it was shown earlier that abundance depends upon recruitment of new size-classes into the catchable population, it must be concluded from the correspondence of size- and year-classes, that fluctuations in abundance result from differences in the strength of the recruited year-classes. It remains to discover what factors are responsible for differences in the strength of scallop year-classes.

RELATIONSHIP BETWEEN ABUNDANCE AND TEMPERATURE

Scallops do not become fully catchable until they are larger than 80 mm. (Fig. 9), therefore, newly recruited year-classes make their first full, and presumably greatest, contribution to the population at the time they pass 80 mm. shell height, or at about the time they have deposited their sixth annulus. If, as has been found in previous studies, the abundance of a year-class is determined at about the time it is being released as eggs by the parent stock, and since abundance of the stocks depends upon recruited year-class strength, then average abundance in any year will be determined by conditions affecting scallop year-classes six years prior to the time they enter the fishery in numbers.

Figure 13A shows the seasonal scallop catch per boat since 1936, which was shown earlier to be a measure of relative abundance of the catchable scallop population. In Figure 13B is shown average temperature of the bottom water of the Bay of Fundy during September, October and November from 1930 to the present, based on monthly observations at 90 metres at *Prince* Station 5 off the entrance to Passamoquoddy Bay. Conditions at this station are representative of conditions in the Bay as a whole (Hachey, 1934). Comparison of abundance with temperature shows that high abundance occurs when temperatures were high, and low abundance when temperatures were low six years previously. The correlation between abundance in individual years from 1936 to 1953, inclusive, and water temperatures from 1930 to 1946⁵ is statistically significant at the one per cent level (0.641 for the 17 years' data).

The correspondence between abundance and water temperature is so close that it is believed to signify an actual relationship between water temperature conditions and population size. The degree to which this influence is important is emphasized even more if certain deficiencies in the original data are considered. For example, because fleet size for 1938-39 was judged from reports of

⁵Water temperature data for *Prince* Station 5 are missing for 1931 and observations for October and November were irregular during the early war years, 1939 through 1942. Values for these periods were calculated as described by Dickie (1953).

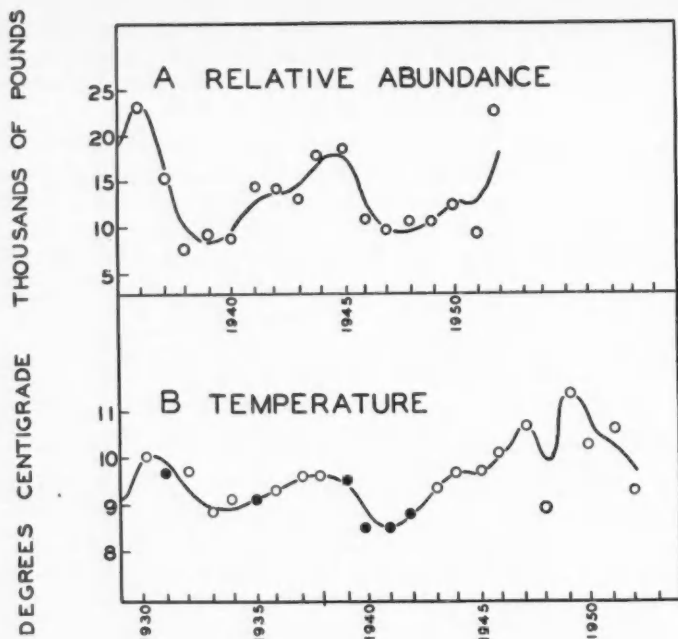


FIGURE 13.—A. Abundance of scallops as shown by seasonal catch per boat. B. Average September-October-November water temperatures at 90 metres at *Prince Station No. 5*, six years previously. (Solid circles indicate that temperature records are incomplete and values given are calculated as shown in Dickie, 1953.)

scallop licences issued for the fiscal year 1938, there is good reason to believe that it is overestimated (p. 801). If this is true, relative abundance in 1938 was not as low as is indicated in Figure 13A. Furthermore, in 1938 a new regulation was introduced limiting the size of the drags, with the result that some of the largest boats which had caught the most scallops were forced to stop fishing. Therefore, the drop in abundance from 1937 to 1938 was probably not as sharp as is indicated by the abundance estimates based on average seasonal catch. Also, relative abundance for 1941–42 is overestimated by catch per boat (p. 836), and a lower abundance figure corresponds better with the temperature trend.

If the relative abundance estimate for 1938 alone is omitted from the comparison, the correlation between abundance and temperature becomes 0.723 compared with the original 0.641. This indicates that, if the errors and deficiencies in the data are accounted for, the correspondence between trends in abundance and temperature will be even better than is indicated by Figure 13. It may be concluded that water conditions related to temperature affect the size of a year-class at about the time it is released as spawn, and are primarily responsible for fluctuations in abundance of the scallops. This conclusion is supported by a more detailed examination of the scallop stocks and ecological conditions in recent years.

YEAR-CLASS STRENGTH IN RECENT YEARS

The strength of recent year-classes may be judged from catches made in standardized hauls during the strip-fishing, and the strength of individual year-classes compared with water temperatures at the time they were spawned. Figure 14 shows the size-composition of the catches made in a series of hauls on Buoy Ground from 1949 to 1953 inclusive, by commercial- and small-mesh drags. Since these size-frequency polygons show the average catch of different size-classes per standard haul, the number of scallops in each fully catchable size-class is a direct measure of its relative strength in the population. The commercial catch polygons are each based on a large number of measurements, as is the small-mesh catch for 1950, and appear to be accurate representations of the size-composition of the stocks. The 1951 to 1953 small-mesh catches are not as accurate, as they are based on relatively few measurements. No samples were taken with the small-mesh drag in 1949.

The 1950 commercial-drag catches from Buoy Ground show a low relative abundance of large size-classes in the catchable population, a stronger 70- to 90-mm. and a weak 45- to 55-mm. size-class. The small-mesh drag catches which include almost all scallops captured down to about 40 mm. size also show the weak larger sizes, but both the 70- to 90-mm. and 45- to 55-mm. size-classes are well represented. These latter size-classes represent the 1945 and 1946 year-classes.

A comparison of the 1950 samples with the 1949 commercial samples shows that the 1945 year-class was present in 1949 as 40- to 60-mm. scallops, and in addition that the 1944 year-class was represented by a weak mode at 60 to 80 mm. The small numbers of the 1944 year-class relative to the strength of the same size-class in later years indicate that it was weaker than the 1945 or 1946 classes and by 1950 was completely overshadowed by them.

The 1951 commercial samples show the 1945 and 1946 year-classes present in some numbers, the 1946 class being the most prominent despite the fact that scallops composing it were still not large enough to be captured with the full efficiency of commercial drags. The 1947 year-class is also represented by a weak mode. From the small-mesh catches the 1946 year-class is seen to have been very much stronger than the 1945 class which appears as a mode from 95 to 100 mm. The 1947 year-class is well represented although it was not yet fully catchable even in the small-mesh drags.

The polygon representing the 1952 commercial samples shows that the 1945 year-class which should be about 90 to 100 mm. is present only as one side of the larger mode at 85 to 95 mm., but is still about equal in strength to any one size-class of older animals. It is overshadowed by the larger 1946 class, which is still distinct from the exceptionally strong 1947 year-class. The small-mesh catch from this year indicates that the 1947 year-class completely dominated the population. However, only one tow was made with it so that the relative strength of the larger size-classes cannot be accurately judged from its catch. An important feature of the 1952 samples is the complete lack of any indication of the 1948 year-class.

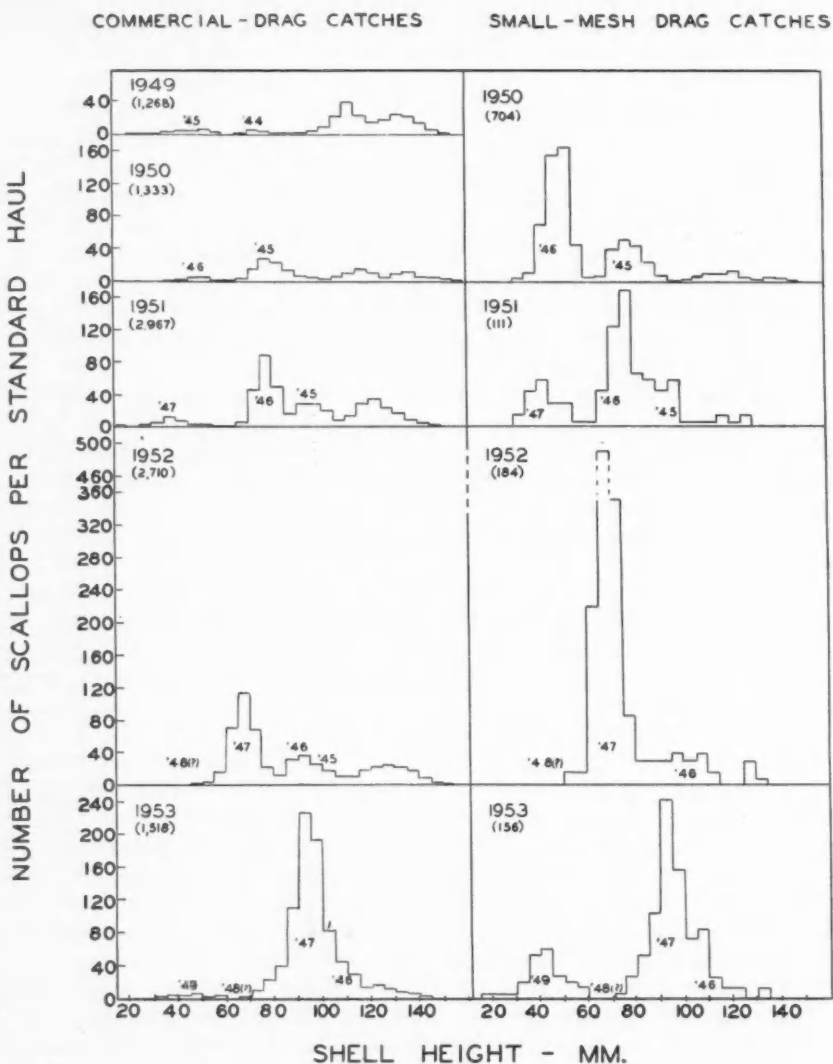


FIGURE 14. Size-frequency and year-class composition of the Buoy Ground scallop stocks. Numbers in brackets under the date show number of scallops in each sample. Year-classes are designated as '44, '45, etc.

The 1953 sampling shows essentially the same picture as that for 1952, although all modes are shifted to the right, reflecting scallop growth, and small scallops representing the 1949 year-class have appeared in the catches.

The samples represented in Figure 14 are all taken from Buoy Ground, which has been used to illustrate relative year-class strength because it is the most heavily fished bed, and as a result fluctuations there are more marked and of more importance to the fishery than are fluctuations on other areas. However, extensive sampling of several beds from 1950 to the present shows that this same situation holds on all Digby scallop beds.

RELATIONSHIP BETWEEN SUCCESS OF YEAR-CLASSES, TIME OF SPAWNING, AND TEMPERATURE

The relative strengths of these recent year-classes may be compared with the average temperatures at the time they were spawned. Average bottom water temperatures during September, October and November were less than 9°C. from 1940 to 1942 and only 9.5°C. in 1943, and no year-class for these years can be detected in the samples of Figure 14. However, 1944, with temperatures of 9.8°C., apparently produced a weak year-class which was present in the 1949 samples. In 1945 average temperature was still 9.8°C. and a stronger set of scallops was produced. In 1946, with a temperature of 10.2°C., the set appears to have been highly successful and in 1947, an average temperature of 10.8°C. seems to have produced one of the most successful year-classes on record. In 1948, average temperature fell sharply to 9.0°C., and no 1948 year-class has yet been represented in any of the commercial- or small-mesh catches. It appears that this year-class, if present in the population, is very weak. In 1949 water temperature was again high (11.5°C.) and the 1953 samples indicate that a strong 1949 year-class is present on the beds.

It must be concluded from the generally good agreement between the relative strengths of recent year-classes and water temperatures in the year they were spawned that the success of sets of scallops is dependent upon the influence of water temperatures or upon environmental conditions related to water temperatures during the early life-history of scallops. A further examination of the data and a review of our knowledge of the life-history of the scallop and of hydrographic conditions suggest what mechanism may be responsible for this relationship.

Observations of the time of scallop spawning have been made by a number of investigators and all agree that spawning begins about mid-July, reaches a maximum in August and September and terminates by late September or early October. The reports of previous investigators are summarized in Table XII.

Observations of the writer for recent years agree with these findings. In 1946 a few scallops on Georges Bank (northwest edge) had begun to spawn as early as June 15, and similarly an occasional spawning or spawned scallop has been observed in the Bay of Fundy in late June and in July. However, in 1949, 1950 and 1952 the main spawning period in the Bay of Fundy was during August and September. In 1949 there was a sharp peak in spawning activity between

TABLE XII. Published records of the time at which scallop spawning takes place.

Year of observation	Place of observation	Method of observation	Spawning period	Authority
1901	Mt. Desert Island, Me.	Microscopic inspection of gonads	After August 20	Drew, 1906
1904 1905 1906 1908 1909	Inshore stations from St. Andrews, N.B., to Seven Islands, P.Q.	Plankton tows	Mid-July to at least Sept. 19. No peak abundance observed	Stafford, 1909
1935 1936	Scallop beds of Digby area	Macroscopic inspection of gonads	Beginning in mid-July, continuing through mid-Sept. with peak in late August and early Sept.	Stevenson, 1936, 1937
1948	Penobscot Bay, Me.	Macroscopic and microscopic examination of gonads	Late August and early Sept.	Welsh, 1950
1949 1950	Cape Cod Bay	Macroscopic examination of gonads	Late September and early October	Posgay, 1950
1949 1950	Penobscot Bay	Macroscopic examination of gonads	July to October with peak in September	Baird, 1953

August 24 and August 27 when the percentage of spent scallops rose from less than one to just over 50 per cent. By September 13, 75 per cent of mature animals were spent. In 1950 spawning began about August 27, and between 45 and 50 per cent were spent by September 8. By September 18 only one unspawned scallop was found in over 100 examined. In 1952 about 50 per cent of those scallops caught from the offshore Digby beds were completely spent by August 19 and the remainder showed signs of partial spawning. According to fishermen, spawning had started about two weeks earlier. Mr. J. S. MacPhail of the Atlantic Biological Station visited the scallop beds off Grand Manan, N.B., on August 19, 1952, and reported that all scallops showed signs of partial spawning (from $\frac{1}{4}$ to $\frac{3}{4}$ spent) although very few were completely spent. It must be concluded that, although the period of maximum scallop spawning activity varies, and high spawning activity probably extends over a period of two to three weeks, it usually begins after the first week in August and is completed by the end of September.

The period of spawning of Bay of Fundy scallops having been defined, it appears that something may be learned about the mechanism responsible for the correlation between abundance and temperature by defining more exactly the period of the year in which water temperatures exert their maximum influence. Figure 15 shows a series of correlation coefficients of abundance of scallops with average water temperatures six years previously. When three-month running

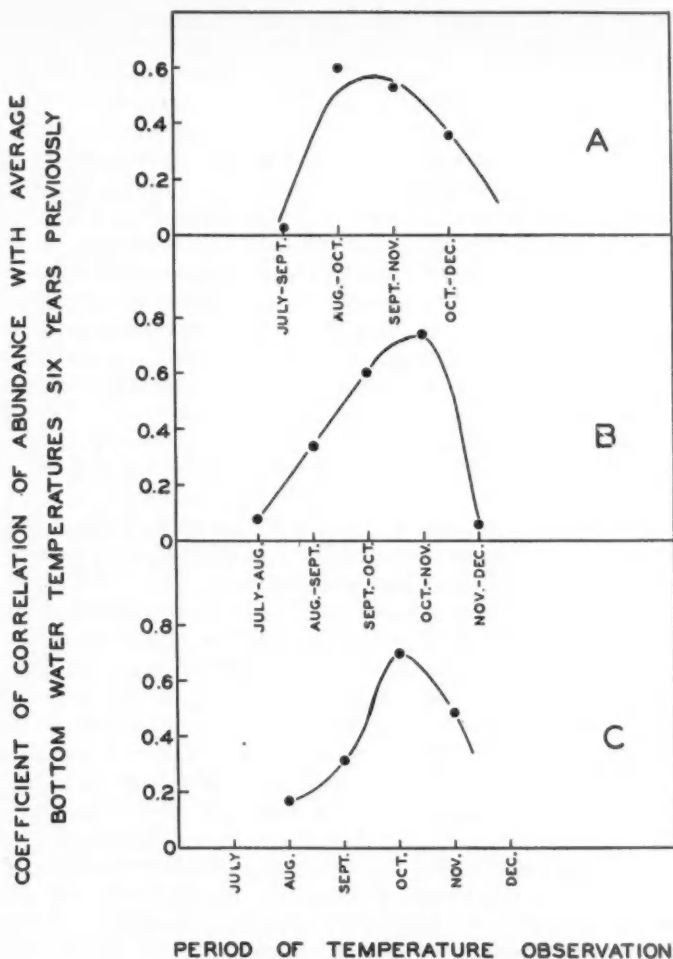


FIGURE 15. Correlation coefficients between relative abundance of the scallop stocks each year from 1937 to 1952, inclusive, and average bottom water temperatures for three- (A), two- (B) and one-month (C) periods six years previously. No temperature data were available for 1931, hence it and 1937 abundance data are omitted here. Correlations are thus based on 16 years' observations.

averages of temperature (Fig. 15A) are used, highest correlations are obtained between abundance and temperatures for August through October and September through November. The period during which temperatures have the greatest effect is even better defined if two-month running averages, or even the monthly

observations, are used. Highest correlations are obtained for the two-month periods of September-October and October-November (Fig. 15B), while correlation with October water temperatures (Fig. 15C) is highest of the single monthly observation comparisons.

Although the period of maximum spawning activity varies from year to year, it is obvious from these comparisons that hydrographic conditions following the period of most active spawning are more important in determining the success of year-classes of scallops than conditions previous to or during spawning. Since this is the period when one would expect to find the year-class present in the water as pelagic larvae, it must be concluded that the success of a year-class is controlled by conditions determining the success of the pelagic larvae in surviving and settling on the parent beds, and conversely that conditions which control production and development of the gonads are relatively unimportant. Some information is available to suggest the nature of the dependence of the pelagic larvae on hydrographic conditions.

RELATIONSHIP BETWEEN HYDROGRAPHIC CONDITIONS AND SURVIVAL OF SCALLOP LARVAE

A number of laboratory observations have been made on scallops and related lamellibranchs, particularly the oyster, which show the general pattern of events of the early life-history and the factors which influence it. Drew (1906) described stages in the development of the giant scallop larvae. He obtained a large number of fertilized eggs from a suspension of eggs and spermatozoa released by mature scallops into the bottom of a dory. He was successful in rearing them to veliger larvae which remained alive for five days. According to his observations the fertilized eggs settled to the bottom of his container where segmentation was initiated in less than an hour. Gastrulae were formed in 12 to 14 hours, actively swimming trochophores in 18 to 20 hours and veligers in 30 hours. Upon formation of the apical tuft of cilia, the trochophores began to move and the trochophores and veligers to swim actively up into the water. The veligers died after about five days, Drew supposes of starvation. It is unfortunate that there are no records of the temperatures at which the larvae were kept.

Stevenson (1936) reared a number of scallop larvae at different temperatures and, although none survived past the trochophore stage, his observations show that temperatures may influence the rate of development and survival of the larvae. He found that at 2.2°C. no development took place and that at 5.0°C. active trochophores are not formed until the sixth and seventh days after fertilization. Development and survival at this temperature were poor, a maximum of only about 33 per cent of the original number of eggs being present as trochophores by the seventh day, with mass mortalities thereafter. At 10.0°C. 12 per cent of the fertilized eggs had become trochophores in three days and a maximum of 37 per cent was reached in five. At this temperature, of the four temperatures used, percentage formation of trochophores was the highest and the trochophores survived for the longest time. At 15.5°C. trochophores were formed by the second day (actually after 43 hours), but only 17 per cent of the fertilized eggs

became trochophores and these survived only one day. It is clear from these observations that rate of development, percentage of eggs developing and length of survival of trochophores were enhanced by increasing temperatures up to about 10°C. Above this, at 15°C., rate of development was more rapid but survival poor.

It may be concluded that temperature has some direct influence on the survival of scallop larvae to, at least, the trochophore stage. However, according to Stevenson's results, the variations in survival between 5°C. and 10°C. were not great. It seems unlikely, therefore, that the striking changes in year-class strength which occur regularly at Digby could be produced by the direct effects of temperature on survival of pelagic larvae. This conclusion is supported by Cole and Knight-Jones (1939) who regard lamellibranch larvae previous to settlement as especially hardy and vigorous, and by the observations of Thorson (1946) who found that pelagic lamellibranch larvae can postpone metamorphosis for long periods of time until suitable bottom is found.

The most important action of temperature appears to be its effect upon the duration of the vulnerable pelagic stages. Medcof (1939), Needler (1941), Korringa (1941) and Loosanoff, Miller and Smith (1951) have shown that small differences in temperature lead to great differences in the length of the pelagic life of oyster and quahaug larvae. Temperatures only a few degrees below those which produce successful year-classes may slow up development of the pelagic stages so much that most of the larvae are devoured by the myriads of filter feeders in the water or are dispersed by water currents before they begin to metamorphose and settle. Thorson (1946) has calculated that a single *Mytilus edulis* filtering 1.4 litres of water per hour may kill 100,000 pelagic lamellibranch larvae in 24 hours at maximum breeding season in a Danish fjord. Korringa (1941) stressed the importance of various filter feeders as predators of oyster larvae, but also showed that failures of sets in the Oosterschelde result from the fact that low temperatures retard larval development and permit a large proportion of the veligers to be carried away by water currents.

No direct observations of the duration of the veliger stage of scallops are available, but Stevenson's observations that temperature has a decided effect on the rate of development of the trochophores are undoubtedly true also for the veliger stages. Low temperatures, then, must prolong the pelagic larval life, at which time Drew found them to be actively swimming about in the water, and must increase the length of their exposure to plankton feeders and to dispersal by water currents. High temperature would speed this phase of development.

Mavor (1922, 1923), Watson (1936), Fish and Johnson (1937) and Hachey and Bailey (1952) have described the circulation of waters in the Bay of Fundy. There is a predominantly counter-clockwise circulation with a current into the bay in deep water and on the Nova Scotian side in the Digby area, a northwest flow across it and an outflow along the New Brunswick shore. But Hachey (1934) has shown that the amount of exchange of Fundy waters with those of the Gulf of Maine varies. In some years the circulation is more or less closed and within

the Bay, and in other years is almost wholly in and out of the Bay. The outside waters from the Gulf of Maine and Scotian Shelf which enter the Bay circulation are of approximately the same temperature from year to year (Bigelow, 1924) and because of the great tidal mixing within the Bay, differences in temperature of the water from year to year are principally a reflection of the amount of irradiation of the surface, and of the resultant interplay of horizontal transport and vertical mixing. If the circulation of water in the Bay is closed, the surface waters warmed by the sun will be thoroughly mixed and the whole water mass will be warmed. If, on the other hand, the circulation is open, the warmed surface waters will be carried away and the average temperature of the water mass will be low. That is, high temperatures reflect a closed circulation and low temperatures an open one.

The part that such circulation and temperature conditions of the Bay must play in the success of year-classes of scallops is obvious. Not only will warm waters hasten development of the larvae to the settling stage, thereby lessening the chances for them to be swept away by the rapid currents, but warm waters are also indicative of a closed circulation, so that dilution of the larvae in the water is confined to the Bay circulation, increasing the chances that they will settle on the beds. On the other hand, cold waters reduce the rate of development of the larvae and are also indicative of an open circulation. This means that at low temperatures the pelagic stages persist for a long time and during this time are more likely to be carried outside the Bay and to be lost to the population. It can only be concluded that this combined action of water circulation and temperature is the mechanism responsible for success of year-classes of scallops, and that it is this mechanism which gives rise to the correlation between fluctuations in abundance and changes in the height of average water temperatures six years previously.

SUMMARY

Fluctuations in total landings have characterized the scallop fishery in the Digby area of the Bay of Fundy since it began in 1920. Landings were high during the 1927-28, 1936-37 and 1945-46 winter fishing seasons and were low in the intervening periods. These fluctuations correspond closely with changes in catch by each boat, indicating that changes in the number of scallops available are primarily responsible for them, and suggesting that there have been natural fluctuations in abundance of the stocks.

Several different methods for assessing the abundance of the stocks are described and discussed, namely changes in commercial catches, special "census-fishing" techniques combined with marking tests to determine efficiency of fishing gear, submarine photographic surveys and a preliminary marking programme. Abundance estimates from the different methods correspond, and indicate that changes in it have been primarily responsible for fluctuations in catch. Abundance was high in 1936, 1944 and 1945, and is at present increasing, and was low in 1939 and 1940, and from 1946 to 1950.

Examination of the stocks present in different years shows that abundance

is high when strong size-classes, representing strong six-year-old year-classes, are being recruited into the catchable population, and is low when recruitment is weak.

Abundance is correlated with average water temperatures six years prior to the time that year-classes enter the fishery in numbers, indicating that abundance and year-class strength are determined by conditions related to water temperature during the early life-history of scallops.

Abundance of the stocks and the strength of year-classes are correlated with water temperatures in the months following the time of spawning, indicating that they are determined by conditions related to water temperatures at the time the scallops are present in the water as pelagic larvae.

Rate of development of the pelagic larvae is known to be influenced by water temperatures and is high at the temperatures which have produced strong year-classes. Water temperatures are also known to be related to the circulation of Bay of Fundy waters. Low temperatures are indicative of great exchange with outside water masses which may disperse the pelagic larvae, but high temperatures are indicative of a relatively closed Fundy circulation which would retain the larvae in the vicinity of the parent beds.

Fluctuations in abundance of the scallop stocks, which are reflected in the fishery, are the result of the combined action of water temperature and circulation on the success of year-classes. Low temperatures retard development of

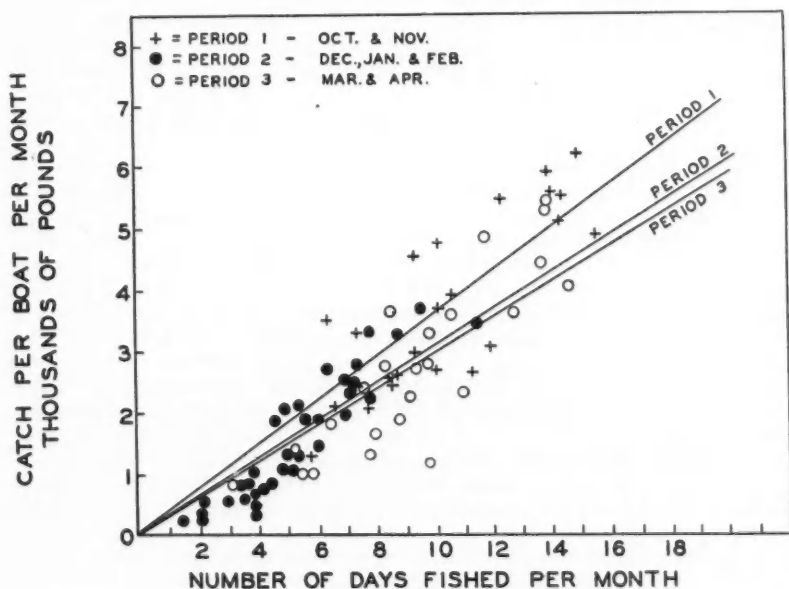


FIGURE 16. Relationship between monthly catch per boat and the number of days fished in three different periods of the season.

the pelagic larvae and water currents at such times disperse them, leading to poor sets, weak year-classes and low abundance of the catchable stocks six years later. High temperatures speed development of the pelagic larvae, and water currents at such times retain them over the parent beds, leading to successful sets, strong year-classes and high abundance of the catchable stocks six years later.

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APPENDIX

THE RELATIONSHIP BETWEEN DAYS FISHED PER MONTH AND MONTHLY CATCH

An analysis of covariance is given below to show the relationship between number of days fished per month (x) and average monthly catch per boat (y) in three different periods during the seven-month scalloping season, based on catch statistics for a sample fleet during the 12-year period 1941-42 to 1952-53 inclusive.

Variation	D.F.	Sum of squares and product			Correction (Σxy) ²	Slope = b = $\frac{\Sigma xy}{\Sigma x^2}$
		Σy^2	Σxy	Σx^2	Σx^2	
Within period	1	24	3793781	101341.4	2823.94	35.8865 = b_1
	2	35	1219245	36690.8	1175.47	31.2137 = b_2
	3	24	2240989	70142.2	2340.33	29.9711 = b_3
Totals	83	7254015	208174.4	6339.74		
	1	23	156991			
	2	34	73988			
	3	23	138752			
Corrected total	80	369731				

$$s^2 = \frac{369731}{80} = 4621.64$$

$$t_{(b_1 b_3)} = \frac{35.8865 - 29.9711}{\sqrt{4621.64 \left(\frac{1}{2823.94} + \frac{1}{2340.33} \right)}} = 3.1129.$$

The analysis indicates that there is a difference in the relationship between monthly catch and days fished per month (i.e. catch per unit effort) in the first two and last two months of the season throughout the 12-year period, independent of the size of the catch. This difference is statistically significant at the one per cent level, as shown by the t value of 3.1 with 44 degrees of freedom.

The Planktonic Copepods (Calanoida, Cyclopoida, Monstrilloida) of Ungava Bay, with Special Reference to the Biology of *Pseudocalanus minutus* and *Calanus finmarchicus*^{1,2}

"CALANUS" SERIES, NO. 8

BY MARION FONTAINE

Eastern Arctic Investigations, Fisheries Research Board of Canada

ABSTRACT

Collections of planktonic copepods of Ungava Bay and central Hudson Strait were made during late June, July and August of 1947, 1949 and 1950. The following 22 species have been identified: *Calanus finmarchicus*, *C. hyperboreus*, *C. helgolandicus*, *Pseudocalanus minutus*, *Microcalanus pygmaeus*, *Gaidius tenuispinus*, *Aetideopsis rostrata*, *Pareuchaeta norvegica*, *P. glacialis*, *Eurytemora americana*, *Metridia longa*, *Pleuromamma robusta*, *Heterorhabdus norvegicus*, *Acartia longiremis*, *A. bifilosa*, *Oithona similis*, *Oncaea borealis*, *Cyclopina gracilis*, *C. schneideri*, *Monstrilla dubia*, *M. helgolandica* and *M. canadensis*. The last 5 species have not previously been recorded from the western North Atlantic. Males of *Cyclopina schneideri* are described for the first time. The two most abundant species, *Calanus finmarchicus* and *Pseudocalanus minutus*, have one generation a year. A small part of the population of *Pseudocalanus minutus* breeds a second time in the autumn. The next most common species, *Acartia longiremis* and *Oithona similis*, probably breed and spawn in July. The population dynamics of all the species are discussed.

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INTRODUCTION

THIS PAPER is a report on the planktonic copepod material collected during the *Calanus* Expeditions, 1947-50, organized by the Fisheries Research Board Eastern Arctic Investigations, in the Ungava Bay area. Only the free-living and semi-parasitic copepods have been included in the species list; the identification of the harpacticoids has been deferred to a later date. Very little information is available on the distribution of copepods in Canadian eastern arctic waters, and no previous study has been made on the life history of any copepod from this area. In studying the production of the waters some insight into the biology of *Pseudocalanus minutus* and *Calanus finmarchicus* is desirable because of the predominance of those two species. *Oithona similis* and *Acartia longiremis* were also plentiful during the three seasons, occasionally forming the bulk of the catches, and a brief study of the life histories of those two species has been included from the 1947 and 1949 results.

At this time of writing, only a bare outline of the bathymetry and hydrography of Ungava Bay has been published (Dunbar, 1951). The field work for a hydrographic study was completed by the *Calanus* in 1949, and the results of this investigation will appear shortly in a paper of this series. The eastern arctic waters include the seas from Cape Farewell to the Strait of Belle Isle, Ungava Bay, Hudson Strait, Hudson Bay, James Bay, Foxe Basin and Channel, the Gulf of Boothia and Prince Regent Inlet, Lancaster and Jones Sounds and the waters between northwest Greenland and Ellesmere Island up to Lincoln Sea. The waters of Ungava Bay are shallow and turbulent, with very strong tidal currents as well as a steady set (described below). The plankton is thus probably a transient population to a great extent, and there can be little doubt that in a summer's work the population from well outside the bay itself is sampled. For the same reason the plankton population of the bay may be taken as a unit, and collecting constantly at the same station will not sample the same individuals.

In its western and southern portions, Ungava Bay is under 100 metres deep, shallower than Hudson Bay. The shoreward half of this portion is less than 50 metres deep. To the east and northeast the Bay deepens to an 800-metre hole just west of the Button Islands. A separate depression in the eastern part of the

bay drops below the 300-metre line, and to the northeast of Akpatok Island, opposite the mouth of Ungava Bay, there is a depression of 600 metres.

The surface waters of Ungava Bay are of low salinity, due to coastal drainage through many small streams, as well as through the George, Whale, Koksoak, Leaf and Payne Rivers. Dunbar in 1947 found salinities everywhere in the coastal regions of Ungava Bay to be lower than 33 per mille, lower than those of Hudson Strait, but higher than the surface waters of Hudson Bay which decrease in salinity from 30 per mille in the north of the bay to 23 per mille in the southernmost portion. Low salinity of Ungava Bay deep-water stations is caused by the turbulence and mixing of the waters, the effect of which is increased by the strong tidal currents. Temperature, salinity and oxygen measurements from the coastal waters of Ungava Bay are given in Table II, page 72 of Dunbar's paper (1951).

The circulation of the waters in the eastern arctic area is cyclonic, or anti-clockwise. Water from Foxe Basin flows southward into Hudson Bay along the western shore, and the outflow from the bay into Hudson Strait moves up the eastern side. The bulk of the Hudson Strait water is composed of the outflow from Hudson Bay, and Ungava Bay is supplied by a surface current which enters from the northwest, crosses to the eastern side south of Akpatok Island, and leaves Ungava Bay in the northeast, rejoining the outflowing water in Hudson Strait. Surface water from Foxe Basin and Hudson Bay enters Hudson Strait at its western entrance; water from Davis Strait and the Labrador Sea enters the Strait at its eastern entrance. This water may contain some admixture of Atlantic (West Greenland) water. This current sets west along the north side of Hudson Strait, east along the south, and is known to reach as far into the strait as Big Island where it turns south and joins the outgoing current along the southern side of the strait. Some of this West Greenland water must also flow into Ungava Bay, as is demonstrated by the Atlantic character of the macroplankton, and by other Atlantic indicators discussed below. There is also hydrographic evidence for the entry of Atlantic water close to the bottom of the bay (Dunbar, personal communication).

MATERIAL AND METHODS

COLLECTION. The copepods were collected during summer cruises from late June to the end of August in 1947, 1949 and 1950. The most complete set of plankton hauls within Ungava Bay was made in 1947, and most of the work of this paper is based on results from that year. In 1949 and 1950, hauling was continued later in the month of August than in 1947, and the results of these years are included here to furnish supporting evidence. While it is not possible to combine the results of the three years into one continuous record, owing to seasonal variations, it is of interest to compare events in the different seasons and a certain amount of corroborating information can be obtained from dates in 1949 and 1950 when no hauling was done in 1947. In 1947 there was a gap in collecting between July 20 and August 10, during which time the dominance of certain stages can only be surmised. Some assistance is provided here in hauls

from the other two years made on July 21 and August 3 and 7. In 1949 and 1950 the *Calanus* worked farther into Hudson Strait and the deeper water at the mouth of Ungava Bay than was possible with the small motorboats used in 1947 (the *Calanus* was built in 1948), and the results of some of the 1949 and 1950 hauls are included for a more complete study of the distribution of the copepods, particularly the vertical distribution.

A station list of the *Calanus* Expeditions, 1947-50, has been published (Dunbar and Grainger, 1951). It is convenient to divide the work of 1947 into two parts. From June 24 to July 20 the expedition collected in the western part of Ungava Bay from north to south at stations 1, 3, 7, 9, 13, 18, 22, and again at station 1 on July 20. From August 10 to 29 the eastern side of the bay was investigated, at stations 31, 33, 37, 38, 40, 41, 43, 44 and 51. Most of the stations were relatively shallow (depths ranging from a few metres to 31 metres). Only four stations were established in deeper water: stations 13 (46-55 metres), 18 (84 metres), 41 (240 metres) and 44 (80 metres).

The entire collection made in 1947 was examined, but from the 1949 and 1950 material hauls were chosen from dates on which no material was available from 1947, and from depths below about 40 metres. In 1949 these included tows from station 103 at the northeast tip of Ungava Bay, but farther west than station 44 in Forbes Sound. A few hauls were taken from station 123 in Calanus Harbour, the Button Islands. On the west coast two overnight hauls were made at stations 124 and 125. A set of hauls is included from station 128, close to the south coast of Akpatok Island and from 126 just north of Payne Bay. Finally, some hauls were examined from station 129, ten miles north of the Koksoak River mouth.

In 1950, hauls were made at stations 209 and 211 in the northwest tip of the Bay, and investigations were carried out in central Hudson Strait at stations 217 (Wakeham Bay) and 222 and 223 (Lake Harbour). The remaining hauls from late August of that year were made at stations 228, 229, 231, 201C and 234, all in Adlorsilik. The stations from which hauls were examined, the nets used and depths of hauling are shown in Table I.

NETS AND TOWS. Horizontal towings were made with fine-mesh nets (Nos. 5 and 6, each one-half metre in diameter; No. 18, 12 inches in diameter), and with coarse nets (Nos. 0 and stramin, each one metre in diameter). One vertical haul was made with the No. 6 net on July 18, 1947 (station 22). A few hauls were made by setting the nets directly in the path of observed tidal currents.

The smaller and younger stages of copepods are normally to be found in the upper levels of water, the larger and older stages in the deeper levels in the daytime. For this reason, as a rule the fine-mesh nets were used in shallow hauls, the coarse nets in deeper hauls. There is, however, considerable overlapping of depths at which the nets were used. The nets are not quantitative, and only relative values were obtained for the maximum occurrence of each stage of the copepods. Since these were not closing nets, some inhabitants of the surface layers will have been included in the deeper hauls as the nets were let down to, and pulled up from, the towing depths.

TABLE I. General information on collection of material.

Date	Sta.	Depth (m.)	No.	Depth of haul (m.)	Net	Time (hr.)	Duration of haul (min.)
24. vi. 47	1	18	1	5	6	1520	25
			2	0	18	1525	20
			3	5	S	1515	30
29. vi. 47	3	28	5	0	18	1205	20
			6	2	S	1200	30
			7	5	6	1204	20
			8	6-7	0	1204	25
3. vii. 47	7	10	10	0	18	1005	20
			11	5-6	0	1000	30
			12	10	S	1000	30
			13	6	6	1004	25
11. vii. 47	9	24	14	15-17	0	1320	30
			15	13	S	1320	30
			16	0	18	1325	20
			17	8	6	1323	25
13. vii. 47	13	46-55	18	36-40	0	0936	30
			19	39	S	0936	30
			20	0	18	0941	20
			21	17	6	0938	28
			22	6	0	1100	30
			23	4-5	S	1100	30
			24	21-17	0	1340	30
17. vii. 47	18	84	25	17-20	6	1345	25
			26	50	S	1340	30
			27	0	18	1345	20
			28	9-11	6	2100	...
20. vii. 47	1	31	29	(vert. haul) 3	6	2120	30
			30	2-1	S	2125	30
			31	5-6	S	1220	30
20. vii. 47	1	31	32	12-14	0	1220	30
			33	8-10	6	1220	30
			34	14-17	S	1317	30
			35	4	6	1317	30
			36	19-21	0	1317	30
			37	0	18	1330	15
			38	0	5	...	60
5. viii. 47	31	shallow-0	39	10-13	S	0910	30
10. viii. 47	33	18-27	40	10-7	6	0910	30
			41	11-9	0	0910	30
			42	0	6	1140	30
11. viii. 47	37	3-4	43	0	S	1148	30
			44	2	6	1635	20
			45	2-3	0	1727	30
16. viii. 47	40	shallow-0	46	0	18	1400	30
17. viii. 47	41	240	47	26-34	6	1400	60
			48	230	0	1400	60
			49	50	S	1400	60
			50	0	18	1435	20
19. viii. 47	44	80	51	42	6	1435	35
			52	73-80	0	1430	40
			53	68-84	S	1434	36
			54	just below surface	5	1530	15
20. viii. 47	43	shallow	55	4	5	1500	15
			56	0	5	...	few min.
			57	2	6	1705	30
			58	4-5	0	1710	30
			59	0	18	1717	20
			60	4-5	0	1755	30
			61	3-4	S	2100	30
29. viii. 47	51	shallow-0	62	6	6	2103	30

TABLE I (Cont'd.)

Date	Sta.	Depth (m.)	No.	Depth of haul (m.)	Net	Time (hr.)	Duration of haul (min.)
6. vii. 49	103	91	63	5-6	S	2145	30
			64	6+	0	2150	30
			4	110	0	...	20
			(touched bottom)				
14. vii. 49	103 (approx.)	103-104 (depth varied)	5	175-200	S	...	25
			8	0	18	1040	15
			9	97-115	S	1030	45
			10	43	6	1033	30
7. viii. 49	103	145-275 (depth varied)	12	5-10	0	1220	12
10. viii. 49	123	15	13	0	18	1225	7
			14	1-7	5	1615	35 (rowing)
			15	0	18	1623	20 (rowing)
			16	10-15	5	1700	5 (rowing)
			17	5-10	0	1745	22
20. viii. 49	124	...	19	0	S	2200	all night
21. viii. 49	125	12	20	0	5	0001	all night
23. viii. 49	126	70-91	22	2-10	S	1157	35
			23	0	18	1202	20
23. viii. 49	126	70-91	24	15	6	1205	30
24. viii. 49	128	185	25	40	0	1545	70
			26	0	18	1620	20
			27	138	S	1555	70
			28	15	S	1440	60
25. viii. 49	129	...	29	0	18	1440	25
			30	5	0	1440	60
			31	10	6	1455	50
			11	75	S	1305	25
21. vii. 50	211	...	14	0	18	1600	20
30. vii. 50	217	18-0	15	1	S	1605	30
			18	1-2	5	...	10 (dinghy near shore)
3. viii. 50	222	80-90	19	0	18	1710	30
			20	1	5	1720	25
			21	7	5	1825	25
			22	8	5	1800	20
25. viii. 50	228	14	27	4	6	...	60
26. viii. 50	229	13	28	1-2	5	1220	60
			29	2-4	0	...	60
			30	12-18	0	1440	20
			31	42-58	0	1110	30
27. viii. 50	231	63-90	32	0	18	1115	18
			33	5-8	6	1117	23
			34	0-1	5	...	90
			35	2-3	6	...	90
			36	90	0	1335	15
			37	13	6	1338	12
28. viii. 50	201C	80-100	38	0	18	1338	12
			39	75-86	0	1000	...
			40	65	6	1020	15

The samples of plankton were preserved in 5% formalin immediately upon pulling up the nets.

SUBSAMPLING. Before examining the collections of copepods, other plankton was removed from the jars. The microplankton, such as cirriped nauplii and annelid larvae, was left with the copepods. A random subsample was obtained by stirring the jar of copepods and, while the contents were still moving, removing one spoonful (7.5 cc.) of copepods. From the first few samples two or three spoonfuls were removed in this way and the copepods of each sorted and

counted. The results tallied remarkably closely, and it was decided that one spoonful would be sufficient, except where the samples were very dilute. In many instances a spoonful was found to be far too large a subsample, and in these cases a dipper was used which scooped out exactly 2 cc. of material at random. About half of the collections from the three years was subsampled, sorted and counted in this way. This method exhausted an enormous amount of time, and many of the subsamples were counted in a chamber marked off in squares to facilitate counting of the whole subsample without sorting. After subsampling, each sample was examined under the lower power of a dissecting microscope for rarer species which might have been missed in the subsampling process.

IDENTIFICATION OF STAGES. With's paper of 1915 was used in identifying the copepodites of *Pseudocalanus minutus* and *Calanus finmarchicus*. The nauplii and copepodites of *Oithona similis* and *Acartia longiremis*, and the nauplii of *Pseudocalanus minutus* were distinguished with the help of Oberg's paper (1906), while Lebour (1916) was consulted for the identification of the *Calanus* nauplii.

Plates I-VIII show histograms of the frequency of each stage of *Calanus*, *Pseudocalanus minutus*, *Oithona similis* and *Acartia longiremis* taken by each net, expressed as percentage of total species numbers (or total genus numbers in the case of *Calanus*). The depth of hauling and net used are included beside each histogram. For economy of space, tables showing the numbers of copepods counted are not included in this publication. However, a copy of the tables containing these data is included in a Master's thesis, which has been bound and catalogued under the same title in the library of McGill University, Montreal.

EXPLANATION OF PLATES








In each plate histograms are shown, from every haul, except where fewer than 25 individuals were counted of the particular species (or genus).

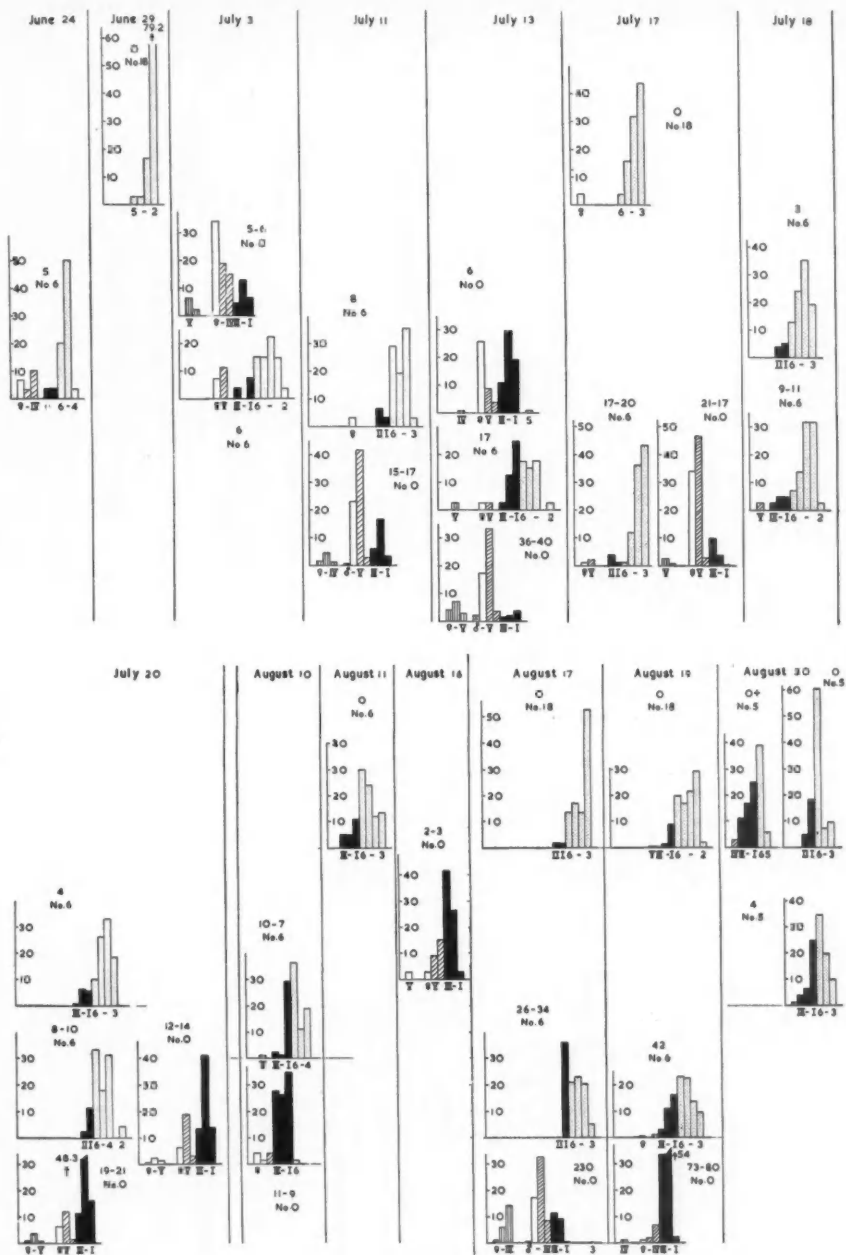
The upper number beside each histogram refers to the depth of hauling, in metres.

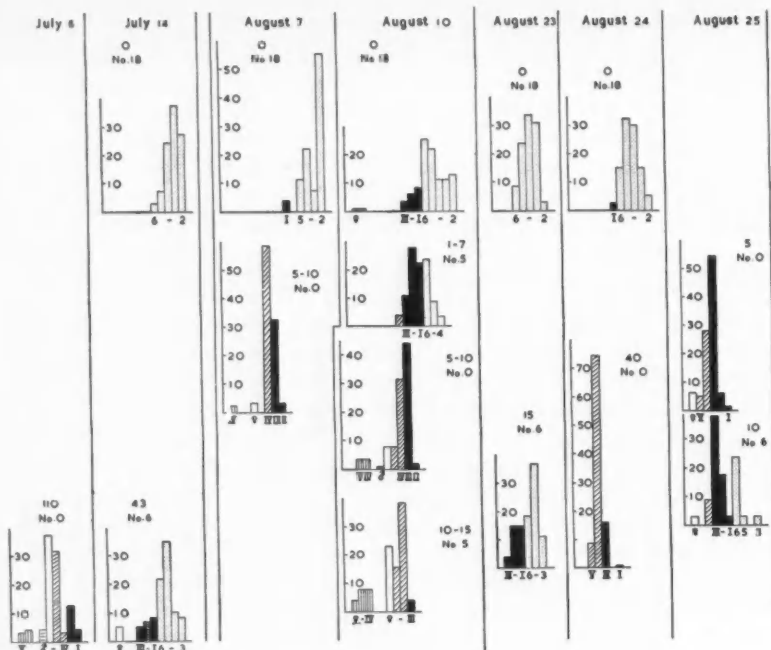
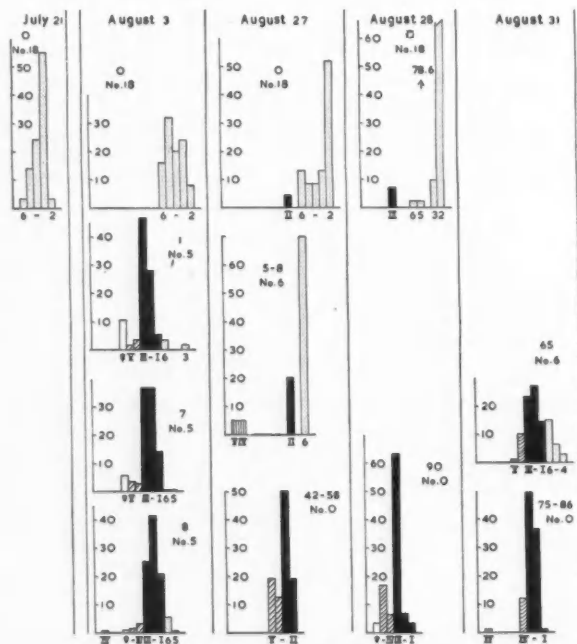
The lower number refers to the type of net used.

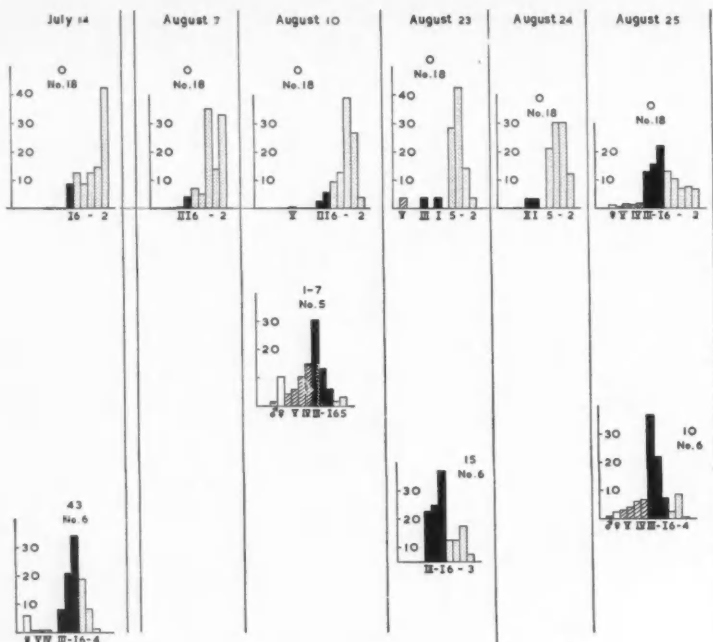
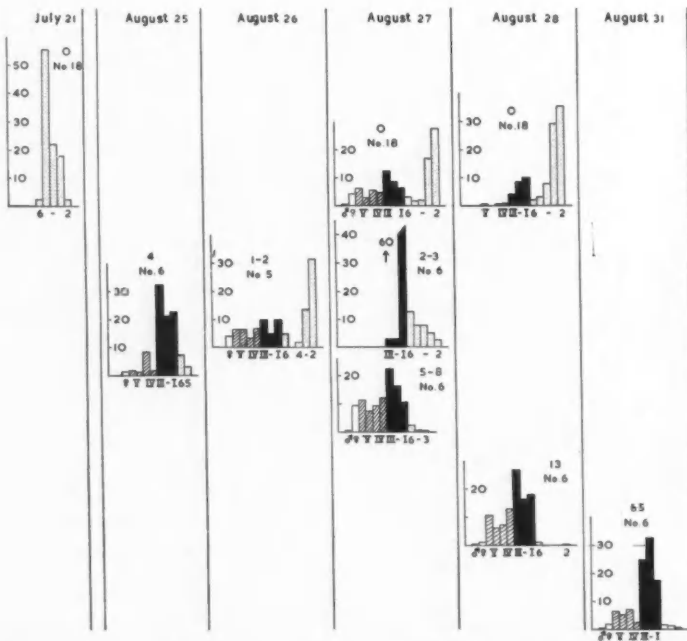
The scale at the left of each histogram shows the percentage of each stage.

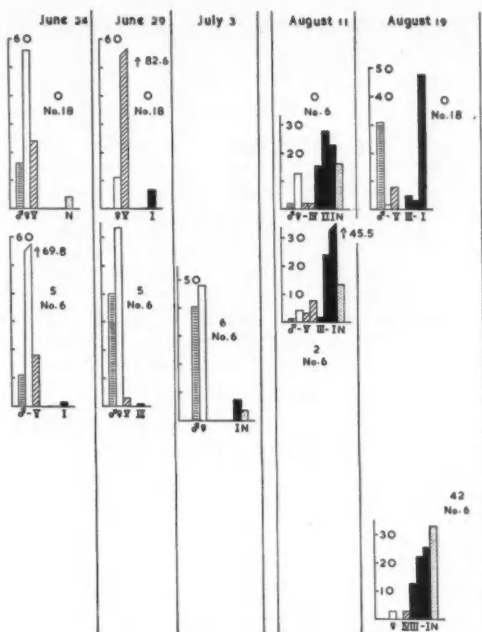
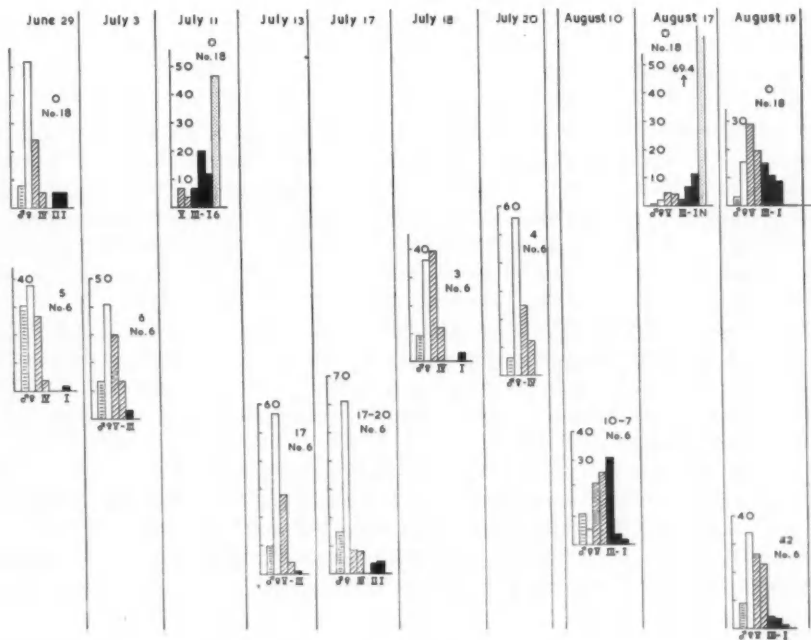
LEGEND FOR HISTOGRAMS

	<i>Calanus hyperboreus</i> , all stages
	Adult males, all other species
	Adult females, all other species
	Stages IV ♂ and V ♂, <i>Pseudocalanus</i> ; stages IV and V, all other species (except <i>C. hyperboreus</i>)
	Stages IV ♀ and V ♀, <i>Pseudocalanus</i>
	Stages I-III, all species
	Nauplii, stages 1-6, all species



PLATE II. *Calanus*, 1949.PLATE III. *Calanus*, 1950.

PLATE V. *Pseudocalanus minutus*, 1949.PLATE VI. *Pseudocalanus minutus*, 1950.

PLATE VII. *Acartia longiremis*, 1947.PLATE VIII. *Oithona similis*, 1947.

SYSTEMATIC ACCOUNT OF THE SPECIES

Family CALANIDAE

Genus *Calanus* Leach*Calanus finmarchicus* (Gunnerus)

Monoculus finmarchicus Gunnerus 1765, p. 175, figs. 20–23.

?*Cetochilus septentrionalis* Goodsir 1843, p. 339, figs. I–II.

Calanus finmarchicus G.O. Sars 1903, p. 9, pls. I–III.

In stages younger than copepodite IV *Calanus finmarchicus* can be distinguished from *C. hyperboreus* only by measuring large numbers of individuals. This was not possible with the Ungava Bay material, and the histograms show percentages of both species. The numbers of *C. hyperboreus* are too small to give anything but an approximation of the biology of the species, but will not be likely to affect the study of *C. finmarchicus*.

DISTRIBUTION IN THE UNGAVA BAY AREA. In 1947 although *Calanus finmarchicus* occurred at stations everywhere in Ungava Bay, it was found in greatest abundance at stations 18, 41 and 44. These were the only stations visited in 1947 at which *Calanus* outnumbered *Pseudocalanus*, probably because of the greater depth of these stations and because the salinities are slightly higher here than anywhere else in the bay.

Calanus finmarchicus occurred in every haul examined from the 1949 material, and was the dominant species at stations 123 and 128. At station 126, although *Oithona similis* was the most abundant species, *Calanus finmarchicus* outnumbered *Pseudocalanus*. *Calanus finmarchicus* predominated in some but not all of the catches from station 103. All these stations were established in the northern part of the bay; at the more southerly stations *Calanus finmarchicus* was replaced by *Pseudocalanus minutus*.

In 1950 *Calanus finmarchicus* was the most abundant species at stations 222 and 223 in Lake Harbour, and in a 65-metre haul from station 234 in Adlorilik. It was not the most numerous species at the northerly stations which were close to shore, as for example 211 and 217.

Calanus finmarchicus is the dominating species in the deeper stations in the northern part of Ungava Bay and into Hudson Strait.

LIFE HISTORY. For presentation of the data, histograms of each net's catch, showing the percentage abundance of each stage of *Calanus* are given in Plates I (1947), II (1949) and III (1950). Stages IV–VI were counted from stramin net subsamples to obtain an indication of their distribution in the deeper layers, but percentages were not calculated. It will be seen from the plates that the distribution of stages was irregular, probably because of currents within the bay, but that a broad outline of the life history can be obtained.

In 1947 adult females were present all summer long but, except for a maximum at 230 metres on August 17, station 41, the numbers decreased markedly during August. Males were always scarce, a few appearing in a stramin net subsample on June 29, station 3, and in the finer nets on July 11 and 13, stations 7 and 13, and August 17, station 41.

Eggs were not counted, but on July 3 only, large quantities of copepod eggs (presumably *Calanus*) were found in the surface catch. Mature females from this material were classified according to Marshall and Orr (1951) as "early", "medium", "semi-ripe", "mature" and "spent" stages. During July nearly all the females (which had been cleared in glycerine overnight) were mature and pre-

sumably producing eggs. If the eggs were fertilized it must have been about a month earlier (or possibly even six months earlier, as Ussing (1938) found to be the case in East Greenland waters). The majority of the females from August 17, station 41, were spent, with semi-ripe and medium stages occurring on August 19, station 44.

Nauplii also occurred all summer long, but, although the percentages of second stage nauplii were large up until July and never disappeared entirely, they were replaced by older stages of nauplii over the course of the summer.

From July 11, station 7, to August 20, station 43, the three stages of small copepodites (I-III) greatly outnumbered the rest of the population of *Calanus*, stage I being usually the most abundant. Copepodites IV of *Calanus finmarchicus* were relatively very scarce in all samples, throughout the 1947 season, but showed peaks on July 3, station 7, at 5-6 metres, and on August 16, station 40, at 2-3 metres. Even on those two days they were outnumbered by the younger stages of the population.

Stage V copepodites showed maxima on July 13 at 36-40 metres, station 13, July 17 at 21-17 metres, station 18, and again on August 17 at 230 metres, station 41. Younger stages dominated the catches from other hauls made on the same days.

The abundance of females in July, with the presence of males, followed by a peak of nauplii suggests that the primary breeding period of *Calanus finmarchicus* in Ungava Bay ends about the last week of June or the first week in July. The females continue to spawn at least until the third week of August. The majority of the population remains in stages I-III from mid-July throughout the autumn, and possibly adults do not appear until early the following year, to breed again in the spring. This annual life cycle compares well with the results of Digby (1954) who found that most of the population of *C. finmarchicus* in Scoresby Sound had but one generation a year. It is impossible to say whether males are equal in abundance to females at the height of the breeding period as they are known to be in temperate waters (Nicholls, 1933), or whether they are never present in large quantities as in East Greenland (Digby, 1954).

The small maxima of stage IV copepodites, the summer peaks in stage V and the presence of males in August indicate that a small part of the Ungava Bay population may moult and breed a second time. The approximate time between the two breeding periods would be about two and a half months, comparable to that described for Norwegian waters (Ruud, 1929) but somewhat longer than the two-month period postulated for temperate waters (Fish, 1936a; Nicholls, 1933; Filteau and Tremblay, 1953).

In 1949 and 1950, nauplii were again present all summer long in the surface layers. Stage III were most abundant on August 25, 1949, station 129, but here again slight maxima of stage IV *Calanus finmarchicus* appeared on August 10 and 24 (Plate II), before the peak of the third stage.

From August 25-31, 1950, stages I-III were most abundant from stations made in Adlorsilik (Plate III). They were also plentiful on August 3 at Lake Harbour, but this is probably too distant for comparison. The results were too

spotty to show peaks of stage IV; there was a maximum of stage V on August 26, station 229, from which adults might have appeared in September.

GENERAL DISTRIBUTION. This species is abundant in polar seas, around Greenland and on the coasts of Norway (Rose, 1933); it has been found along all the coasts of Iceland (Jespersen, 1940); on the American side of the Atlantic it is found as far south as New York (Bigelow, 1915), but the species was not taken south of 40° north latitude in either the Atlantic or the Pacific by the *Carnegie* (Wilson, 1942); it was found by the *Albatross* in the South Atlantic as far south as 48°37' south latitude, 65°46' west longitude. The same expedition took the species at the Galapagos, in the Bering Sea, the Gulf of Alaska, off Hokkaido, Japan, in the Okhotsk Sea and off Peru (Wilson, 1950); it is present in the waters around the Chu-San Archipelago (Sproston, 1949); in the northern area of the Arabian Sea (Sewell, 1947); it also occurs from the coasts of New Zealand to Auckland and the Campbell Islands and is common in Melbourne Harbour, Australia (Farran, 1929).

Calanus helgolandicus (Claus)

Cetochilus helgolandicus Claus 1863, p. 171, pl. XXVI, figs. 2-9.

Calanus finmarchicus Giesbrecht 1892, pl. 8, fig. 31, figs. 20-21.

Calanus helgolandicus Sars 1903, pp. 11-12, pl. IV; Rees 1949, pp. 219-222, fig. 1.

The status of this form, whether separate species, or a subspecies of *Calanus finmarchicus*, has not yet been decided.

No representatives were noted during the first examination of the copepod material from Ungava Bay. However, re-examination of the subsamples resulted in the identification of one *Calanus helgolandicus*, copepodite IV, from station 44.

GENERAL DISTRIBUTION. *Calanus helgolandicus* is well known from British waters: from the North Sea and off Plymouth (Rees, 1949; Russell, 1951) and from Millport, Scotland (Marshall, Orr and Rees, 1953); it has been found on the coast of France (Rose, 1933); the Mediterranean (Giesbrecht, 1892); the Norwegian coast (Sars, 1903); Tromsø Fjord (Marshall, Orr and Rees, 1953); Chesapeake Bay (Wilson, 1932); the coast of California and off Peru (Wilson, 1950). Wilson (1932) quotes Karawjew as having found the species in the Black Sea, and Brady as including it from the fauna of the Australian coast.

Calanus hyperboreus Krøyer

Calanus hyperboreus Krøyer 1838, p. 84, pl. IV, fig. 23; G. O. Sars 1903, p. 12, pl. V.

DISTRIBUTION IN THE UNGAVA BAY AREA. In every haul made in 1947 the numbers of *Calanus hyperboreus* were exceedingly small. It was taken at station 1 on July 20, and at stations 7, 9, 13, 18, 22, 33, 41, 44 and 51. It was not found at any station where the depth was less than 10 metres (except station 51, where it composed 0.2% of the copepod population). Every stage was plentiful on July 17, at station 18, and on August 17 at station 41.

In 1949 and 1950 when it was possible to make deeper hauls, a large number of *C. hyperboreus* was taken at station 128, just south of Akpatok Island, and at station 209 at the northwest tip of the bay. Apart from these two hauls the occurrence of *C. hyperboreus* was extremely limited, though it occurred in small numbers at most other stations.

No adult males were found at any time, in any of the three years of hauling. It may be that this species is brought in by currents but does not breed in the bay, or it may spawn in the deeper parts much earlier than the time of collecting by the *Calanus* Expeditions. The time of spawning may be similar to that of *C. hyperboreus* off Möre, where it spawns only once, from February to March (Ruud, 1929). In Ungava Bay the three stages (copepodites IV-VI) were found at all depths even up to the level of 2 metres, but any numbers larger than 100 were taken below 15 metres.

GENERAL DISTRIBUTION. According to Rose (1933) this species occurs in the North Atlantic, east of Ireland and the polar sea; it is also common along all the coasts of Iceland (Jespersen, 1940), and along the east and west coasts of Greenland (Jespersen, 1934, 1939). It is distributed over the whole of Baffin Bay and extends southward on the American side of the Atlantic as far as Cape Cod (Bigelow, 1915); on the European side of the Atlantic it is known from Norwegian coasts (Sars, 1903) and the coast of France (Rose, 1933). It was taken from the Bering Sea, off Hokkaido, Japan and south of the Galapagos in the Pacific Ocean by the *Albatross* (Wilson, 1950).

Family PSEUDOCALANIDAE

Genus *Pseudocalanus* Boeck

Pseudocalanus minutus (Krøyer)

Calanus minutus (Krøyer) 1849, p. 543.

Clausia elongata Boeck 1864, p. 234.

Pseudocalanus elongatus Boeck 1872, p. 37.

Pseudocalanus major G. O. Sars 1900, pp. 69-72, pl. XX.

Pseudocalanus gracilis G. O. Sars 1903, pp. 134-35, pl. I (suppl.).

Pseudocalanus minutus With 1915, p. 67, pl. I, fig. 8; Wilson 1932, pp. 43-44, fig. 25.

DISTRIBUTION IN THE UNGAVA BAY AREA. This species was present at every station visited in and around the bay and was the dominant species at most. At station 9, however, the surface catch was composed principally of *Oithona similis*, rather than of *Pseudocalanus*. At station 18, where hauls were made on July 17, 1947, it was outnumbered by *Calanus*. In the surface haul made at station 41, on August 17, it was outnumbered by *Calanus*, while *Oithona similis* was more plentiful than either of them; but at this station at 230 metres *Pseudocalanus* represented 63.6% of the copepod population as compared to 29.4% *Calanus*. The values obtained for *Pseudocalanus* and *Calanus* from the surface haul from Forbes Sound (station 44) on August 19 were nearly equal, and *Oithona similis* was only a little more abundant. Considerable numbers of *Pseudocalanus* were found at station 51 between the George and the Whale Rivers, where *Calanus* was absent almost entirely. The salinity at this tidal station was low and *Pseudocalanus* was outnumbered by brackish water species (*Acartia biflosa* and *Eurytemora americana*) in some of the hauls. Probably *Pseudocalanus* was brought in by currents from farther north in the bay to mingle with the indigenous brackish water fauna in this area.

In 1949, at stations farther north at the mouth of Ungava Bay, and at station 128 just south of Akpatok Island, *Pseudocalanus* was found in quantities equal to or slightly smaller than *Calanus*, whereas in the more southern stations and at Adlorilik it was still the prevalent species. At stations 222 and 223 at Lake Harbour, visited in 1950, *Calanus* outnumbered *Pseudocalanus*, and very few specimens of the latter genus were found in the subsamples.

The 1947 hauls were used as the basic material for studying the biology of *Pseudocalanus*. Adult females, males and nauplii were found at every station, and from every station except 33 (where few females occurred), 41 and 44 (at 230 and 73-80 metres), some of the females were ovigerous. Judging from the continuous presence of females (with or without eggs), accompanied by a continuous presence of adult males and nauplii, it is evident that *Pseudocalanus* breeds all summer long in Ungava Bay. It is well known that *Pseudocalanus* has the ability to adapt to wide thermal and salinity ranges, and it is therefore not surprising that it can breed in the shallow coastal waters as well as in the deeper more central and eastern parts of the bay. It has been found breeding in the neritic regions of the Gulf of Maine, and in these regions it also outnumbers *Calanus* (Fish, 1936b).

LIFE HISTORY. In spite of the continuous breeding of *Pseudocalanus*, it was possible to estimate the length of the developmental period, and breeding times,

because of the enormous increase in production at the end of June, the effects of which can be traced throughout the time of hauling. In the histograms showing the relative abundance of the stages of *Pseudocalanus* (Plates IV-VI) only the values obtained by the fine-mesh nets were used, because these are the only ones which catch all the stages. Stages V and VI, taken by the No. 0 net were also counted to obtain some information on the occurrence of those stages at levels deeper than those reached by the fine nets.

Adult females were present throughout the summer in 1947. They were abundant from June 24 to July 11, but showed a marked decrease from July 13 till August 11, when the numbers increased slightly.

Adult males were always scarce but showed small maxima on June 24, station 1, and August 29, station 51. Where stage V copepodites were plentiful, the males were usually about equal in numbers to the females and it is probable that the difference in proportion of the two sexes of adults is due to a differential mortality rate, rather than to a smaller production of adult males. This is similar to the situation at Loch Striven where the numbers of adult males are always small in proportion to the females, but where males and females of stages IV and V copepodites are usually present in equal quantities (Marshall, 1949). The longer-living adult females may produce several batches of eggs as is the case with *Calanus* (Marshall and Orr, 1951).

Nauplii were plentiful all summer long. Second stage, which predominated on June 29, and July 3 and 11, stations 3, 7 and 9, were replaced by later stages of nauplii from July 13 to August 19. There was an apparent decrease on August 20, station 43, and August 29, station 51, but this may have been due to the position of the stations in shallow water close to shore.

The small copepodites, stages I-III, appeared in large quantities on July 11, station 7, with a maximum on July 13, station 13. The relative numbers of these stages remained high until the end of August. Stages I and II outnumbered stage III in most of the catches.

Stage IV copepodites were always scarce, but on August 11, station 38, showed a very small maximum which was masked by the continued presence of smaller copepodites. The No. 0 net towing at 230 metres and at 73-80 metres on August 17 and 19, stations 41 and 44, brought up large catches of stage V copepodites, probably produced by the stage IV copepodites of August 11. The unusual depth at which these copepodites were found suggests that the fifth stage may have undergone a downward vertical migration as it is known to do in summer in the Gulf of Maine (Fish, 1936b).

Some of these fifth stage copepodites may have contributed to the slight increase of adults found at station 51 on August 29. The presence of ovigerous females indicates the beginning of a second much smaller breeding peak or "autumn bloom" of *Pseudocalanus*. Since the period of most active breeding in the spring may be assumed to be somewhat earlier than June 24, the period between breeding peaks can be estimated as about nine weeks. This period between broods is slightly longer than the six weeks to two months described for temperate waters (Fish, 1936b; Marshall, 1949; Digby, 1950), and more

comparable to the two-month period suggested by Ruud (1929) for the waters off Möre.

The continued abundance of small copepodites until August 29 in Ungava Bay is evidence that the majority of the population developed much more slowly than the individuals mentioned above. The difference in rate of development may be due to a slight cooling of Ungava Bay waters in late August. Presumably the products of later spawning (after the June peak) in July and early August cannot mature in the time available before the second peak. This slow development of a large part of the population of *Pseudocalanus* is similar to the results of Digby (1954) working in East Greenland waters. He found that, although most of the population had but one generation a year, a few individuals might pass from egg to adult in one summer season, and he was able to show that a part of the population probably had a 1½-year life cycle.

Adults were scarcer in 1949 than in 1947 (Plate V), but increased in numbers slightly on August 21, station 125, and August 25, station 129. Nauplii however, were plentiful during July and August. As in 1947 the most abundant stages were stage I-III copepodites which had not disappeared by the time hauling ceased. There was no maximum of stage V copepodites to compare with the August maxima of 1947, but the No. 0 net was not used in the deeper layers during this time, except on August 24, station 128, when the water was sparsely populated with *Pseudocalanus*.

Stage I-III copepodites again dominated the August hauls made in 1950. On August 27, at 42-58 metres, station 231, large quantities of stage V copepodites were taken in the No. 0 net. Fewer were caught by the fine nets in the upper layers, but even in these hauls they outnumbered the adults (Plate VI). They continued to be plentiful on August 28, at 90 metres, station 201C, and on August 31, at 75-86 metres and at 65 metres, station 234.

It appears that most of the population of *Pseudocalanus* remains as copepodites I-III until the end of August, and may winter over in late copepodite stages, not reproducing until the following spring. Some of the population (probably from the June spawning) develop more quickly during July and August, stage V appearing in mid-August to the end of the month, and breeding adults in late August, or early September. This annual breeding cycle of *Pseudocalanus* with a small part of the population breeding in the autumn is similar to the developmental periods known for East Greenland waters (Ussing, 1938; Digby, 1954).

SIZE OF ADULT AND FIFTH STAGE FEMALES. In an attempt to separate the populations of *Pseudocalanus* according to size-groups, adult females were measured from subsamples taken on June 24, 29, July 3, 13, 20 and August 11 of 1947, and fifth stage females were measured from June 24, 29 and August 11 subsamples. In each case the cephalothorax was measured, and all measurements, except those of the adult females from June 29, July 3, 13 and 20, were made with an ocular micrometer of which the smallest division equalled 17.5μ. Adult females from the subsamples mentioned above were measured at the British

Museum (Natural History) with an ocular micrometer whose smallest division equalled 25μ . The populations were analysed graphically using mathematical probability paper (Harding, 1949).

The mean lengths and standard deviations plotted from probability paper are given in Table II. Figures 1 and 2 show the analyses made on probability paper from June 24 (Fig. 1) and August 11 (Fig. 2). In the figures the crosses and broken lines denote the populations of adult females, the squares and line R show the bimodal resultant of the adult population in Figure 1. The points M, M_1 and M_2 , where the population lines cut the vertical for 50% correspond to the mean lengths of the populations. The white histograms to the left of the figures give the size distributions of the adult females; the stippled histograms superimposed on them show size distributions of the fifth stage females. Analyses of the fifth stage populations were made on the same paper and are shown by circles in the figures.

TABLE II. Mean lengths (mm.) of *Pseudocalanus* females, adults and stage V copepodites.

Date	Stage V ♀		Stage VI ♀	
24. vi. 47	1.076 ± 0.016	3%	1.044 ± 0.080	50%
	0.958 ± 0.018	42%	0.762 ± 0.044	50%
	0.880 ± 0.027	45%		
29. vi. 47	1.085 ± 0.044	8%	1.017 ± 0.055	70%
	0.980 ± 0.020	22%	0.730 ± 0.050	30%
	0.866 ± 0.026	70%		
3. vii. 47			1.016 ± 0.087	65%
			0.725 ± 0.040	35%
13. vii. 47			1.081 ± 0.085	65%
			0.750 ± 0.044	35%
20. vii. 47			1.016 ± 0.059	35%
			0.713 ± 0.047	65%
11. viii. 47	1.271 ± 0.060	16½%	1.142 ± 0.075	
	1.081 ± 0.030	50%		
	0.945 ± 0.031	33½%		

The populations of the June and July females were bimodal (Fig. 1, Table II), the mean length of the larger individuals approximately 1.4 times that of the smaller. The population of August 11 females was unimodal (Fig. 2, Table II), with a mean length longer than that of either of the June and July populations.

The results of the measurements of the fifth stage females are more difficult to interpret. At first glance the curves appear to be uni-modal (Figs. 1 and 2) with mean lengths of 0.945 mm. ± 0.1 (June 24); 0.955 mm. ± 0.135 (June 29); 1.094 mm ± 0.105 (August 11). However, a better fit is obtained by analysing them as polymodal populations (Table II). Probably the populations of fifth stage copepodites are indeed polymodal, but the numbers measured are too small to be sure that this is the case and for this reason the population curves have not been included in the diagrams.

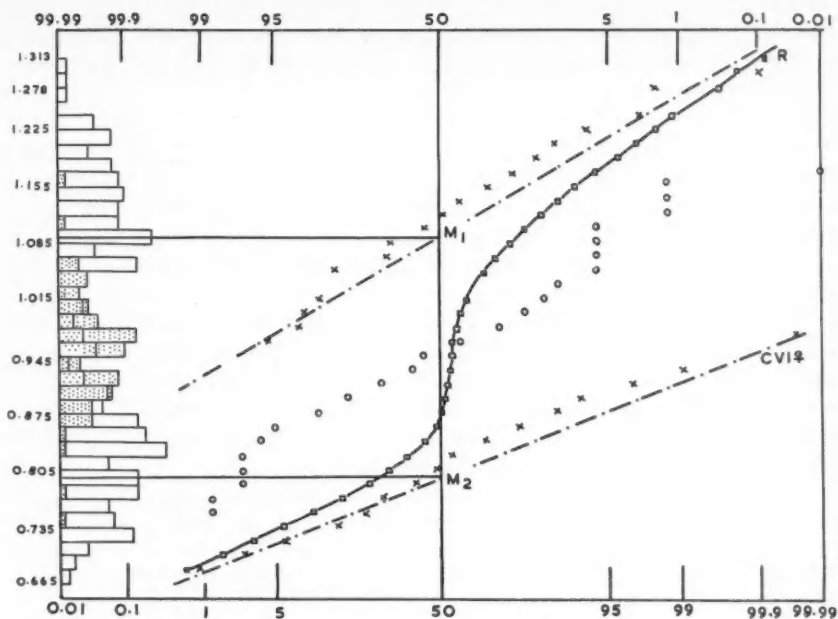


FIGURE 1. Size of *Pseudocalanus* females from June 24, 1947. (See page 876 for details.)

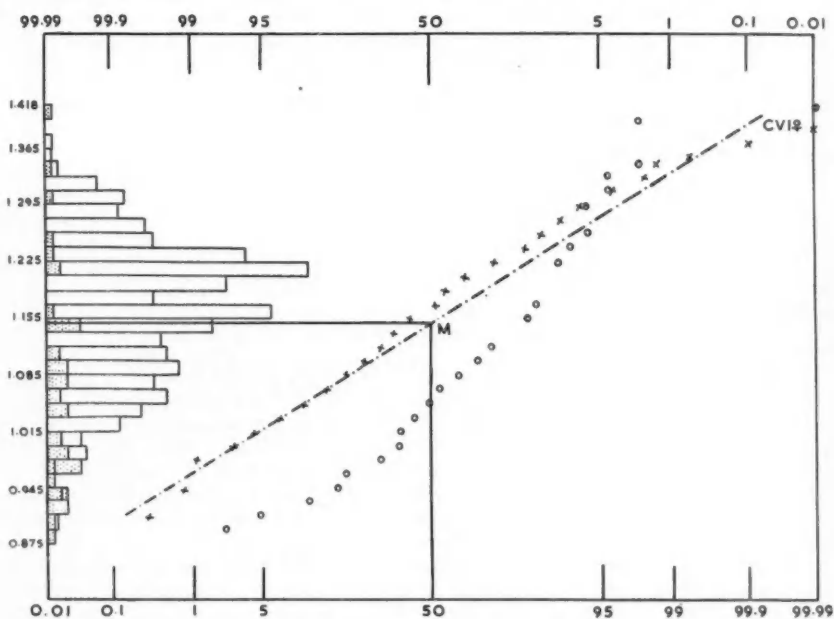


FIGURE 2. Size of *Pseudocalanus* females from August 11, 1947. (See page 876 for details.)

The extremely wide range in size of Ungava Bay *Pseudocalanus* is comparable with that found in population studies made in other areas (Størmer, 1929; Marshall, 1949; Digby, 1950, 1954). An increase in size during the summer months has been shown to occur in these regions. Digby (1954) points out that in East Greenland, where temperatures vary little throughout the year, size change is a function of the available phytoplankton. There are no quantitative data yet available on diatom production in Ungava Bay, but the surface catch made on July 13, 1947, consisted almost solely of diatoms. Possibly this was a peak in phytoplankton production which might have aided in producing larger individuals later in the summer.

The polymodal size distributions of both stages of *Pseudocalanus* in this material might possibly be accounted for by the mixing of the waters. Measurements of smaller stages of copepodites are needed to confirm this. Since polymodal curves were also obtained in other regions, it is more likely that it is due to an overlapping in production of the two groups, and that smaller individuals have not died off before larger ones are produced.

GENERAL DISTRIBUTION. This species is both arctic and subarctic in distribution, and is known from Alaska, the Arctic Ocean (Willey, 1920); Greenland, Iceland, Faroe Islands (With, 1915); the Norwegian coast (Sars, 1921); North Sea (Möbius, Timm, in Wilson, 1932); on the American side of the Atlantic, it is known as far north as northern Baffin Bay (Jespersen, 1923), and as far south as Chesapeake Bay (Wilson, 1932); in the Atlantic and Pacific Oceans it was taken at every locality visited by the *Carnegie* (Wilson, 1942).

Genus *Microcalanus* G. O. Sars

Microcalanus pygmaeus G. O. Sars

Pseudocalanus pygmaeus (female) Sars 1900, p. 73, pl. XXI.

Spinocalanus longicornis (male) Sars 1900, p. 77, pl. XXII, figs. 13-14.

Microcalanus pusillus Sars 1903, p. 157, Suppl. pls. I-III; v. Bremen 1908, p. 27, fig. 25.

Microcalanus pygmaeus v. Bremen 1908, p. 27, fig. 24; With 1915, p. 66.

DISTRIBUTION IN THE UNGAVA BAY AREA. This species was caught in very small numbers during the three years of sampling. It was taken in quantities of less than 1% in the following tows: in 1947 at stations 3 (5 metres), 13 (17 metres), 1 (on July 20, 8-10 metres) and 44 (42 metres); in 1949 at stations 103 (43 metres), 123 (1-7 metres); in 1950 at station 231 (5-8 metres). Examination of the whole samples showed the occurrence of a very few at station 232 in 1950 at 0-½ metre. All these were adult females, except for one stage III copepodite and two stage IV copepodites.

GENERAL DISTRIBUTION. Very small numbers were also recorded from West Greenland waters by the *Godthaab* Expedition (Jespersen, 1934), but it is a commonly occurring copepod in East Greenland waters (With, 1915; Jespersen, 1923; Størmer, 1929). These workers recorded it at depths from 800 to 50 metres, and only rarely at the surface. Digby (1954), however, found that copepodites and adults are most common in the surface layers of Scoresby Sound over the spring and early summer months, but that the population sinks to below 50 metres after June. The presence of the species above 50 metres in Ungava Bay may be a further indication of the turbulence of the waters.

Microcalanus pygmaeus is a rather pronounced arctic form, penetrating in the deeper water layers fairly far south in the Atlantic. It has been found in the West Wind Drift and in the south polar region, swept by the North Atlantic intermediate current from the Atlantic

Ocean to the Antarctic (Sewell, 1948). Jespersen (1940) found it everywhere along the coast of Iceland, more frequently on the north coast. It is well known from Baffin Bay to Davis Strait, and in the sea immediately to the south, but Ungava Bay is its southern limit along the American side of the Atlantic. *M. pygmaeus* was found at only two stations in the tropical Atlantic by the *Carnegie* (Wilson, 1942), but was abundant in the Pacific. It is also found in the Japanese fauna, probably having drifted southwards in the Oya-Shio current (Sewell, 1948).

Family AETIDEIDAE G. O. Sars

Genus *Gaidius* Giesbrecht

Gaidius tenuispinus (G. O. Sars)

Chiridus tenuispinus Sars 1900, p. 67, pl. XVIII.

Gaidius borealis Wolfenden 1903, p. 365.

Gaidius tenuispinus Sars 1903, p. 162, pl. XVIII, Suppl. pl. VI.

DISTRIBUTION IN THE UNGAVA BAY AREA. This species was taken at station 41, where one copepodite stage IV and three copepodites stage III were found in 1947. In 1949 one adult ovigerous female was found at station 103, and one adult female without eggs was caught between stations 103 and 104. The hauls which caught this species were all made in deep water.

GENERAL DISTRIBUTION. This deep-water species is common in West Greenland waters where it was taken by the *Godthaab* Expedition at a large number of stations, from the south point of Greenland to the northern part of Baffin Bay and Smith Sound (Jespersen, 1934). It is also common in Davis Strait, Denmark Strait and around Iceland (With, 1915), being most common on the south and west coasts (Jespersen, 1940). It is known from both sides of the Atlantic Ocean; on the American side its distribution extends as far south as the Gulf of Maine (Bigelow, in Wilson, 1932); it has been reported as far south as the area northwest of the Canary Islands (Scott, 1909). It has also been found in antarctic seas between 66° and 76° south latitude (Farran, 1929).

Genus *Aetideopsis* G. O. Sars

Aetideopsis rostrata G. O. Sars

Aetideopsis rostrata G. O. Sars 1903, p. 160, Suppl. pls. V-VI; Wilson 1932, p. 46, fig. 27.

DISTRIBUTION IN THE UNGAVA BAY AREA. One adult female was taken between stations 103 and 104, towing at 175-200 metres, in 1949.

GENERAL DISTRIBUTION. This is a rare deep-water species, first recorded by Sars (1903) from 500-1,000 metres, between Jan Mayen and Finmark in 1900. It has been found from western Ireland to distinctly arctic waters (Sars, 1903; Bernstein, 1932); on the American coast of the Atlantic Ocean one specimen has been reported northeast of Cape Cod Light (Wilson, 1932). Small numbers were taken by the *Godthaab* Expedition in the southern part of Davis Strait and in a few places in Baffin Bay.

Family EUCHAETIDAE

Genus *Pareuchaeta* A. Scott

Pareuchaeta norvegica (Boeck)

Euchaeta norvegica Boeck 1872, p. 40; Sars 1903, p. 38, pls. XIV-XVI.

Pareuchaeta norvegica A. Scott 1909, p. 69; Wilson 1932, p. 65, fig. 43.

DISTRIBUTION IN THE UNGAVA BAY AREA. A few specimens of adults and stage V copepodites were found in the material. Three adult females, one ovigerous, were found in the subsamples at station 41, 1947, together with one stage III, two stage II and one stage I copepodites of some species of *Pareuchaeta*. From the same year one adult female was found in the subsamples of station 44, and one copepodite V was found on examining the entire sample from 4 metres at station 43. In 1949, between stations 103 and 104, there were 8 females (2 bearing spermatophores), and 2 males in the subsamples. From 103, there were 2 adult females and 6 stage V copepodites. There were no specimens of *Pareuchaeta* found in the 1950 material.

GENERAL DISTRIBUTION. This species is fairly common along the whole Norwegian coast (Sars, 1903) and is known from the Polar Sea, north of Spitzbergen, to a latitude of 84° north (Jespersen, 1934); it is common along the entire coast of East Greenland, in the interiors of fjords as well as the more open coastal waters (Jespersen, 1934, 1939). It was taken by the *Godthaab* Expedition at most of the stations in West Greenland waters, but in larger numbers in the water south of Davis Strait (Jespersen, 1934); on the American coast of the Atlantic it has been found as far south as Chesapeake Bay (Wilson, 1932).

Pareuchaeta glacialis (H. J. Hansen)

Euchaeta glacialis Hansen 1886, p. 74, pl. XXVII, fig. 5, pl. XXIV, fig. 1.

Pareuchaeta glacialis Sars 1903, p. 40, pl. XXVII; Jespersen 1934, pp. 75-78.

DISTRIBUTION IN THE UNGAVA BAY AREA. Two adults were found in the 1949 material: one (female) from station 103, hauling at 110 metres; one (male) from between stations 103 and 104, hauling at 175-200 metres.

GENERAL DISTRIBUTION. In contrast to *P. norvegica*, *P. glacialis* is a distinctly arctic form found in the Polar Basin and common in the polar areas east of Greenland, in Denmark Strait, and in the eastern part of the Atlantic north of 60° north latitude; between Iceland and the south point of Greenland it is found only in a deep layer of polar water immediately off the east coast of Greenland. It is common in Baffin Bay and Smith Sound (Jespersen, 1934), but south of Davis Strait it is found in considerable numbers only in the western area (close to Resolution Island) where the cold Labrador current flows southward.

Family TEMORIDAE

Genus *Eurytemora* Giesbrecht

Eurytemora americana Williams

Eurytemora americana Williams 1906, p. 645-47, figs. 8-11.

Eurytemora thompsoni Willey 1923, p. 314.

Eurytemora transversalis Campbell 1930, p. 179, pl. 1, figs. 4, 5, 6.

Eurytemora kieferi Smirnov 1931, p. 196, figs. 1-5.

Eurytemora thompsoni Lowndes 1931, p. 501, figs. 1-10.

Eurytemora americana Lowndes 1932, p. 541, figs. 1-11; Wilson 1932, p. 109, fig. 72; Gurney 1933, Appendix, pp. 369-373, figs. 2048-2061.

DISTRIBUTION IN THE UNGAVA BAY AREA. One adult female with ovisacs, but no eggs, was taken at station 1, June 24, 1947. From just below the surface at station 37 were one stage II, two stage III and one stage V copepodites. Large numbers of males and females of the species and of *Eurytemora* copepodites, presumably *E. americana*, were found in hauls made at station 51. About 40% of the females were carrying spermatophores, and a few bore the

remains of egg sacs. Males were present in quantities about equal to the females. Station 51 was established on the coast of Ungava Bay between the mouths of the George and the Whale Rivers. The water is brackish (the station is dry at low tide); *E. americana* was greatly outnumbered by *Acartia biflosa* at this station.

GENERAL DISTRIBUTION. *Eurytemora americana* is a brackish water species which was first described by Williams (1906), from specimens found in Narragansett Bay from January to April, and in summer, in Charles Town Pond, a brackish inlet from the ocean. Variations of it have been reported from Plymouth, Lancing and Sandown, England. Gurney (1933) includes *E. thompsoni* Lowndes from Lancing, and *E. kieferi* Smirnov, found off Kamchatka and in the Sea of Okhotsk, under the species *E. americana* Williams. He points out also that *E. transversalis* Campbell from Vancouver Island is identical with the above species, with the exception that, in the male, exopod 2 of the left fifth foot is shown with the apex segmented and reflexed in Campbell's drawing.

Family METRIDIIDAE

Genus *Metridia* Boeck

Metridia longa (Lubbock)

Calanus longus Lubbock 1854, p. 127, pl. V, fig. 10.

Metridia armata Boeck 1864, p. 14.

Metridia longa Sars 1903, p. 112, pls. LXXV-LXXVI.

DISTRIBUTION IN THE UNGAVA BAY AREA. In the deeper hauls made in Ungava Bay, *Metridia longa* was a commonly occurring copepod. All stages of copepodites appeared frequently in the subsamples. In 1947 it was caught at stations 7, 9, 13, 19, 22 and 41. In 1949 it occurred at stations 103, between stations 103 and 104, and at station 123. In 1950 it was taken at station 234 only, hauling at 75-86 metres.

The largest quantities of specimens were caught below 100 metres. Compared to the other species, the largest proportions of *M. longa* were taken at station 103, hauling at 110 metres, where it made up 21.1% of the total aggregate of copepods. This station was visited on July 6, 1949, and at that time (in the subsample) the proportion of adult males to adult females was exactly equal. The species was also plentiful between stations 103 and 104 in 1949, where it composed 8.6% of the total number of copepods, and at station 41, in 1947, where it formed 7.8% of the total. The species was most common, therefore, in the north-eastern part of the bay. In the 230-metre haul from station 41, August 17, 1947, the population of adults comprised 65.1% males to 34.9% females. There is probably a breeding period of *Metridia longa* from July to August and possibly it continues later in the season. In hauls made at depths under 100 metres, the species was taken in quantities of less than 4% of the total copepod population.

GENERAL DISTRIBUTION. *Metridia longa* is widely distributed over the northern seas, from pronounced arctic regions to fairly far south. In the more southern latitudes it occurs most often only at fairly great depths. It was recorded by Sars (1925) as far south as the Azores; by Wilson (1932) as far south as the Woods Hole region on the American Atlantic coast; it is common in West Greenland waters (Jespersen, 1934) and East Greenland waters (Ussing, 1938); all along the coast of Iceland, usually above 200 metres in the intermediate water layers (Jespersen, 1940); along the whole Norwegian coast, Faroe Channel, Spitzbergen and Polar Basin (Sars, 1903). It is also known from the Indian Ocean, and was captured by the *Carnegie* at one station in the North Pacific (Wilson, 1942); it is also found in the Japanese area (Sewell, 1948); it is an arctic form, epi-planktonic in the Antarctic (Russell, 1935, in Sewell, 1948, p. 395).

Genus *Pleuromamma* Giesbrecht*Pleuromamma robusta* (Dahl)

Pleuromamma robusta F. Dahl 1893, p. 105.

Pleuromamma robusta Sars 1903, p. 115, pls. LXXVIII-LXXIX; Steuer 1932, p. 20, figs. 69-91.

Pleuromamma rotundum Esterly (Bigelow 1905, p. 287, quoted in Jespersen, 1934).

Pleuromamma wolfendeni Brady 1918.

Pleuromamma robusta Jespersen 1934, p. 102-103.

DISTRIBUTION IN THE UNGAVA BAY AREA. Two adult females were found in the entire collection. They were taken at station 41, hauling at 230 metres on August 17, 1947.

GENERAL DISTRIBUTION. *Pleuromamma robusta* is the species of *Pleuromamma* met with farthest north (Jespersen, 1934). It has been found in the waters between Iceland and Norway in the Faroe Channel, and west of Ireland (Sars, 1903); and several times as far north as Lofoten; around Iceland it occurs most frequently off the south and west coasts, showing that the northern limit occurs off the northwestern point of Iceland (Jespersen, 1940); it has also been found off the southernmost point of Greenland and in the sea south of Davis Strait (Jespersen, 1934). It has been recorded from the east coast of North America to the east of Newfoundland and in the region of Woods Hole (Wilson, 1932). Apparently this is a fairly southern form which may have been carried into Ungava Bay by currents entering Hudson Strait from the direction of West Greenland.

Family HETERORHABDIDAE

Genus *Heterorhabdus* Giesbrecht*Heterorhabdus norvegicus* (Boeck)

Heterochaeta norvegica Boeck 1872, p. 40.

Heterochaeta profundus Dahl 1893, p. 105.

Heterorhabdus norvegicus Sars 1903, p. 118, pls. LXXX-LXXXI.

DISTRIBUTION IN THE UNGAVA BAY AREA. One adult female of this species was taken at station 41 hauling at 230 metres on August 17, 1947; two adult females were found between stations 103 and 104, hauling at 175-200 metres; and one adult male was found at station 103 at 97-115 metres. These were the deepest hauls made during the three years.

GENERAL DISTRIBUTION. *Heterorhabdus norvegicus* is distributed over most of the northern Atlantic and the adjoining arctic seas in the Polar Basin and Faroe Channel (Sars, 1903). It is a northern form, but has been recorded as far south as the vicinity of the Canaries by the Prince of Monaco (Jespersen, 1934); it has been captured on the Norwegian coast in deep water (Sars, 1903) and along all the coasts of Iceland, chiefly above fairly deep water and never in fjords (Jespersen, 1940). It has also been found on the American coast of the Atlantic as far south as Woods Hole (Wilson, 1932).

Family ACARTIIDAE

Genus *Acartia* Dana*Acartia longiremis* (Lilljeborg)

Dias longiremis Lilljeborg 1853, p. 181, pl. XXIV.

Acartia longiremis Sars 1903, p. 149, pls. XCIX-X.

Acartia longiremis spiniremis Pinhey 1927, p. 186.

Adult male specimens of *A. longiremis* from Hudson Strait have been found to possess a strong spine or seta on the inner side of the second basal joint of the left fifth foot (Pinhey,

1927, p. 186). Pinhey, who found this seta in all males from the Pacific and Atlantic coast of North America, named the males *Acartia longiremis*, ssp. *spiniremis*. Sixteen specimens from Ungava Bay were dissected from stations 1, 3, 7, 9, 18, 40, 44 and 51. All were found to agree with Pinhey's description and drawing.

DISTRIBUTION IN THE UNGAVA BAY AREA. This species, the fourth most common in the area, was taken at the following stations in 1947: 1, 3, 7, 9, 13, 18, 22, 31, 33, 37, 38, 40, 41, 44, 43 and 51. *Acartia longiremis* is usually found above 20 metres in Ungava Bay; maximum abundance of the species occurred at the end of June and in the middle of August in 1947.

In 1949 it was caught at stations 103, 123, 126, 128 and 129; in 1950, at stations 211, 222, 223, 228, 229, 230, 231, 232, 201C and 234. Like *Pseudocalanus* it is tolerant of the fairly low salinities, of the southern part of Ungava Bay, Adlörilik and Payne Bay.

REPRODUCTION AND DEVELOPMENT. Adult males were present at every station during July and August, 1947 (Plate VII). Probably *Acartia longiremis* behaves very like *Pseudocalanus* in Ungava Bay, that is, adults and nauplii never disappear entirely, and there is fairly continuous breeding during the summer. This is comparable to the life history of *Pseudocalanus* and *Acartia clausi* in Loch Striven (Marshall, 1949) and at Plymouth (Digby, 1950).

The greater abundance of males than females in June and early July suggests that June 24 to July 3 was the beginning of a breeding peak. Adults were present in smaller proportions in August than in June and on August 19 males were far more abundant than females. Possibly the sexes alternate in maximum abundance as they do in the Nordåsvatn Fjord (Wiborg, 1944).

The period of main spawning probably takes place in the middle of July. Although we have no data from this period, young copepodites were present in maximum quantities on August 11 and 19, stations 37 and 44. The breeding peak of *Acartia longiremis* in Ungava Bay occurs about two weeks later in the summer than that of *Pseudocalanus minutus*.

The population of *Acartia longiremis* was not analysed from the 1949 and 1950 hauls. However, two adult females from July 14, 1949 and August 3, 1950 were bearing spermatophores; many *Acartia* nauplii were taken in the August hauls from these two years.

GENERAL DISTRIBUTION. *Acartia longiremis* is a circumpolar, distinctly northern form, met with as far north as the area around Spitzbergen and the Polar Basin, north of the New Siberian Islands (Sars, 1903); it is known from west European waters southward to the English Channel. It is of frequent occurrence along all the coasts of Iceland, though it does not appear in great numbers along the northeast coasts until the late summer (Jespersen, 1940); found everywhere along the eastern coasts of Greenland; in Baffin Bay it has been reported farther north on the western side than on the eastern side. Its Atlantic distribution extends south to the Sargasso Sea and the Caribbean, but in the *Carnegie* Pacific hauls it was confined to a few stations, north of the Samoan Islands (Wilson, 1942). In the North Pacific it has been found on the North American coast and in the Arctic Ocean, near Alaska (Willey, 1920).

Acartia bifilosa (Giesbrecht)

Dias bifilosus Giesbrecht 1881, p. 257; v. Bremen 1908, p. 158, fig. 175; Steuer 1923, p. 110, figs. 99-101.

DISTRIBUTION IN THE UNGAVA BAY AREA. A few specimens (two adult females, one fifth stage male) were taken at station 1, at 5 metres, and two females, one adult the other stage V copepodite were taken at station 38 at 2 metres. Very large numbers of the species

were found at station 51, between the Whale and the George Rivers. Here it composed most of the plankton and was found in association with *Eurytemora americana*. Males, females, copepodites and all younger stages down to first stage nauplius of *Acartia* (presumably *A. bifilosa*) were found at this station. Males were present in quantities equal to the females, and many of the females were bearing spermatophores.

GENERAL DISTRIBUTION. This species is of limited distribution and is found throughout the Baltic, in the English Channel, the North Sea between Scotland and Norway, and on the Dutch coasts, but was not included by Sars in the fauna of Norway. It is a characteristically brackish water and estuarine species, though it has been recorded from the open sea. Cleve (1900) records it from the mouth of the Congo and gives its range as between 6° and 63° north latitude. It has been reported from the Faroe Channel and northeast Scotland (Gurney, 1933). It was not mentioned by Jespersen as occurring in the fauna of the coasts of Greenland; one specimen was recorded by Gran (1902) in the fauna around Iceland at a point 66°34' north latitude. On the American coasts of the Atlantic it is common in Woods Hole Harbour from December to June (Fish, 1925). Deevey (1948) records *A. tonsa* and *A. clausi* from Tisbury Great Pond, but makes no mention of *A. bifilosa*.

Family OITHONIDAE

Genus *Oithona* Baird

Oithona similis Claus

Oithona similis Claus 1866, p. 14; Sars 1918, pp. 8 and 207, pl. III.

DISTRIBUTION IN THE UNGAVA BAY AREA. This is the only species of *Oithona* found in Ungava Bay, and is common in the bay, occasionally outnumbering all other species. In 1947 it occurred at the following stations: 1, 3, 7, 9, 18, 22, 31, 33, 37, 38, 41, 44 and 43.

In 1949, it was taken at stations: 103, 123, 125, 126, 128 and 129.

In 1950, *Oithona similis* was captured at stations 211, 217, 222, 228, 231, 217, and 234.

Oithona similis is most abundant at or near the surface. At stations 18, 41 and 44 in 1947 it outnumbered both *Calanus* and *Pseudocalanus* in the surface hauls, or above 20 metres, while much smaller numbers were taken below 20 metres. In 1949 and 1947, the species was present in maximum numbers in the middle of August, but in 1950 the maximum occurred towards the end of the month.

REPRODUCTION AND DEVELOPMENT. *Oithona similis* is similar to *Pseudocalanus* and *Acartia longiremis* in that adult males are present throughout the summer in Ungava Bay, and presumably breeding is continuous. The males were outnumbered by the females in every 1947 haul, except for a small sample taken on August 10, station 33 (Plate VIII). Males are also always much scarcer than females at Loch Striven (Marshall, 1949). The proportion of females during July was large and the high numbers of nauplii occurring on July 11 indicate active spawning during the first week of July. The products of this spawning appeared as small copepodites in August, with a large number of nauplii still present in the waters on August 17, at station 41.

In 1949, large numbers of small copepodites occurred during the middle of August, again suggesting a spawning period during July.

GENERAL DISTRIBUTION. *Oithona similis* is circumpolar in distribution and is found in polar seas and everywhere in the North Atlantic and North Pacific. It is widely distributed in the Pacific (Wilson, 1942), and found on both coasts of North America. It is abundant in

the Gulf of Maine, but south of Cape Cod it is gradually replaced by *O. brevicornis* on the American coast (Fish, 1936a). It is common on the Norwegian coast (Sars, 1918) and in British waters (Digby, 1950; Marshall, 1949) and has been reported from the Bay of Biscay (Rose, 1933). It has also been found in the Antarctic Ocean (Sars, quoted in Wilson, 1932) and from the Red Sea and Indian Ocean (Thompson and Scott, in Wilson, 1932). Among the Ungava Bay individuals, many were of a short squat shape described by Wiborg (1944), but it was not possible to determine whether they were a variety of *Oithona similis* or a different subspecies.

Family ONCAEIDAE

Genus *Oncaea* Philippi

Oncaea borealis G. O. Sars

Oncaea borealis Sars 1918, p. 191, pl. CVIII.

DISTRIBUTION IN THE UNGAVA BAY AREA. This copepod occurred in many hauls, but always in small numbers; the greatest proportion was 2.8% from station 234 in 1950. In 1947 it was taken at the following stations: 9, 13, 18, 22, 31, 33, 37, 38, 41 and 44. In all these hauls the quantities of *Oncaea borealis* were less than 1%, except from the 42-metre haul at station 44, where the species composed 1.4% of the total number of copepods.

In 1949 *Oncaea borealis* was found at station 103 and at station 129.

In 1950 it was taken at five stations: 228, 231, 232, 201C and 234. In the last, fairly deep haul, the proportion to other copepods was somewhat greater (2.8%) but the tow was of short duration and possibly *Oncaea* was captured as the net was taken out of the water. The small numbers of *O. borealis* found in Ungava Bay are probably accounted for by the low salinities of the area. Johnson (1953) has pointed out that in the seas around Alaska the species is most common in areas of higher salinities and lower temperatures.

The quantities captured in Ungava Bay were too small to determine the breeding time of *Oncaea borealis*, in 1950 at stations 231 and 232, visited on August 27, three pairs of males and females were found together in copulation. Males were present in the waters during the two months of July and August of 1947, and breeding is probably continuous during the summer.

GENERAL DISTRIBUTION. This is an arctic form, known from polar seas as well as from the North Atlantic. In the *Dana* material it was found in hauls from Kajer Franz Joseph and Scoresby Sound Fjords (everywhere in small quantities) and was common in Denmark Strait; it is also found along the entire coast of East Greenland (Jespersen, 1939); it has been taken in West Greenland waters from the southernmost areas to the most northern part of Baffin Bay (Jespersen, 1923; Størmer, 1929); it is common in Departure Bay, near Vancouver Island (Campbell, 1929); it has been found in the Bering Sea, Bering Strait and Chukchi Sea (Johnson, 1953).

Family CYCLOPINIDAE

Genus *Cyclopina* Claus

Cyclopina gracilis Claus

Cyclopina gracilis Claus 1863, p. 104, pl. X, figs. 9-15.

Cyclopina norvegica Boeck 1864, p. 247.

Cyclopina gracilis Brady 1880, p. 93, pl. 24B, figs. 1-9, pl. 91, figs. 10, 11.

Cyclopina gracilis Giesbrecht 1882, pp. 137-139, figs.

Cyclopina salinus Brady 1900, p. 432, figs.

Cyclopina gracilis Gurney 1933, Vol. III, p. 8.

In members of this species found in Ungava Bay, there is a variation in the shape of the distal segment of the fifth foot (Fig. 3), which although bearing the same number and type of appendages as those pictured by Sars (1903, pl. IV), is very much rounded and possesses hairs on both lateral edges.

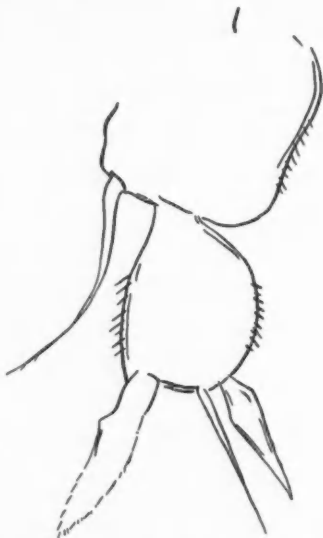


FIGURE 3. Fifth foot of *Cyclopina gracilis* from Ungava Bay ($\times 315$).

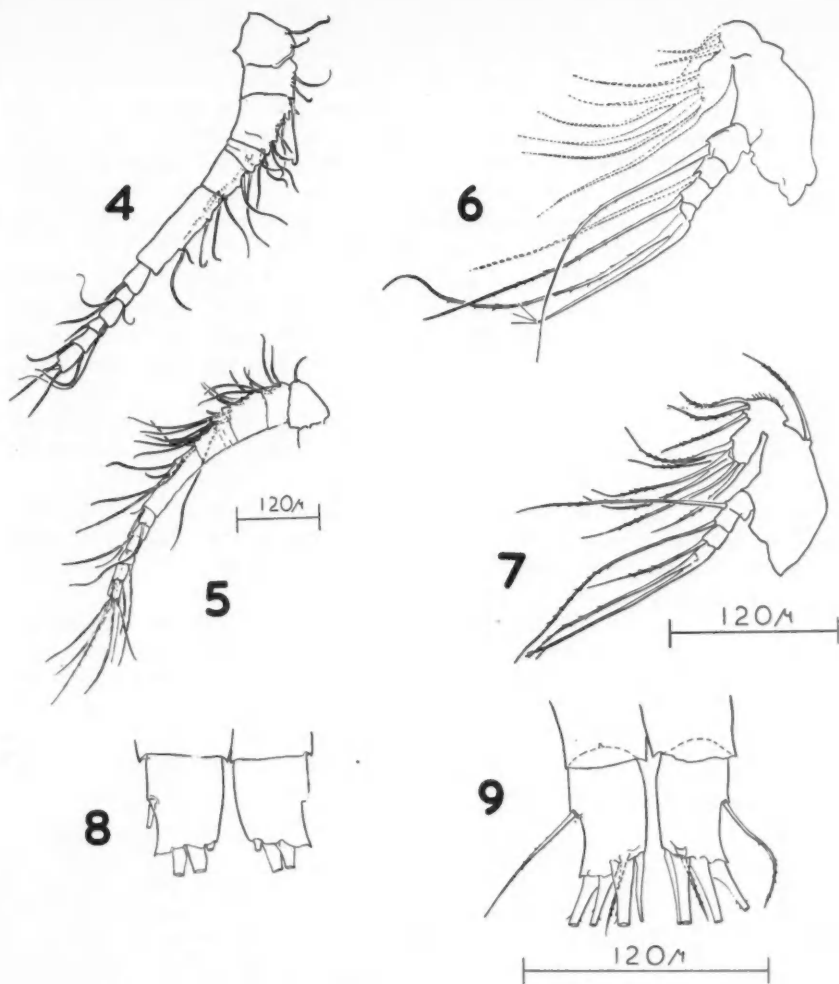
DISTRIBUTION IN THE UNGAVA BAY AREA. Females of this species were found in a few hauls in Ungava Bay, always in quantities of less than 1% of the total number of copepods. It was not taken at any station visited during 1949 or 1950, but was found in hauls made at the following stations in 1947: 3, 9, 13, 22 and 38.

GENERAL DISTRIBUTION. *Cyclopina gracilis* is with difficulty distinguished from *C. norvegica* Boeck. According to Gurney (1933) *C. norvegica* is a strictly littoral variety of the typical *C. gracilis*, which is marine. *Cyclopina gracilis* has been reported from polar waters and the Norwegian coast (Sars, 1918); it was found by Claus in the Mediterranean (Gurney, 1933), and in the Black Sea (Czerniawsky, in Gurney, 1933); and is known from the Suez Canal (Sewell, 1949) and has been found as far south in the Pacific Ocean as the Malay Archipelago. This is apparently the first record for the species in the western North Atlantic.

Cyclopina schneideri T. Scott

Cyclopina schneideri T. Scott 1903, p. 6-7, pl. I, figs. 1-6; Schäfer 1936, in key.

Females of this species were described for the first time by Thomas Scott (1903) from material collected in arctic seas. The specimens were found in small numbers in Vadsö Sound, East Finmark. Scott described the antennule as composed of 12 joints, six of these being small end joints. The segmentation of the antennules is not clear, and since it is difficult to distinguish the segments, a



FIGURES 4-9. *Cyclopina schneideri* Scott ♀ : 4. Antennule of type specimen. 5. Antennule of Ungava Bay specimen. 6. Mandible of type specimen. 7. Mandible of Ungava Bay specimen. 8. Caudal rami of type specimen, ventral view. 9. Caudal rami of Ungava Bay specimen, ventral view.

drawing of the antennule of Scott's type specimen, deposited in the British Museum (Natural History), (Fig. 4) was made to compare with that of the Ungava Bay female (Fig. 5). It will be seen that the fourth segment is not perfectly separated from the fifth in the Ungava Bay specimens and that no suggestion of a seventh segment following the long sixth segment as pictured in Scott's fig. 2, pl. I was easily visible.

The palps of the mandibles are shown in Figures 6 (type specimen) and 7 (Ungava Bay specimen). Scott portrayed the end segment of the four-jointed endopodite as bearing two plumose setae. Dr. Harding of the British Museum (Natural History) (personal communication) has drawn attention to the fact that the terminal seta of the fourth segment is in fact non-plumose, but bears a small tuft of hairs at the tip, a character common among the species of *Cyclopina*. The exopodite of the mandibular palp, and the seta on the second segment of the endopodite, were missing in Scott's type specimens. These have been drawn in dotted lines from more of Scott's material.

Scott did not show the lateral spines on the caudal rami which are present in both the type specimen (Fig. 8), and in the individuals from Ungava Bay (Fig. 9). In a key given by Schäfer (1936) the caudal rami are described as being as long as they are wide. Examination of the type specimen has shown that they are slightly longer than they are wide.

Three females from Ungava Bay measured 1.0325 mm. One measured 1.0150 mm. These lengths compare well with the Vadsö Sound females which were somewhat longer than a millimetre.

The occurrence of this species in Ungava Bay marks the first record from the American side of the Atlantic. Males of the species have not previously been discovered from any area. Males were of frequent occurrence in Ungava Bay samples containing females of *C. schneideri*.

The description of the males is as follows. Length: 0.7175 mm. The antennules are 15-segmented, geniculate between the 13th and 14th segments (Fig. 10). The antennae (Fig. 11) are composed of the four segments typical of species of *Cyclopina*; the terminal segment of each antenna bears seven setae. The mandible (Fig. 12) is identical with that of the female.

Legs 1 to 4 possess three-segmented rami with the following numbers of spines and setae on the segments:

	P ₁		P ₂		P ₃		P ₄	
	Exp.	End.	Exp.	End.	Exp.	End.	Exp.	End.
Spines	1:1:4	---	1:1:4	---	1:1:4	---	1:1:3	---
Setae	1:1:4	1:1:5	1:1:5	1:2:6	1:1:5	1:2:6	1:1:5	1:2:5

This spine-seta formula is identical with that of the female. The first leg of the male is shown in Figure 13.

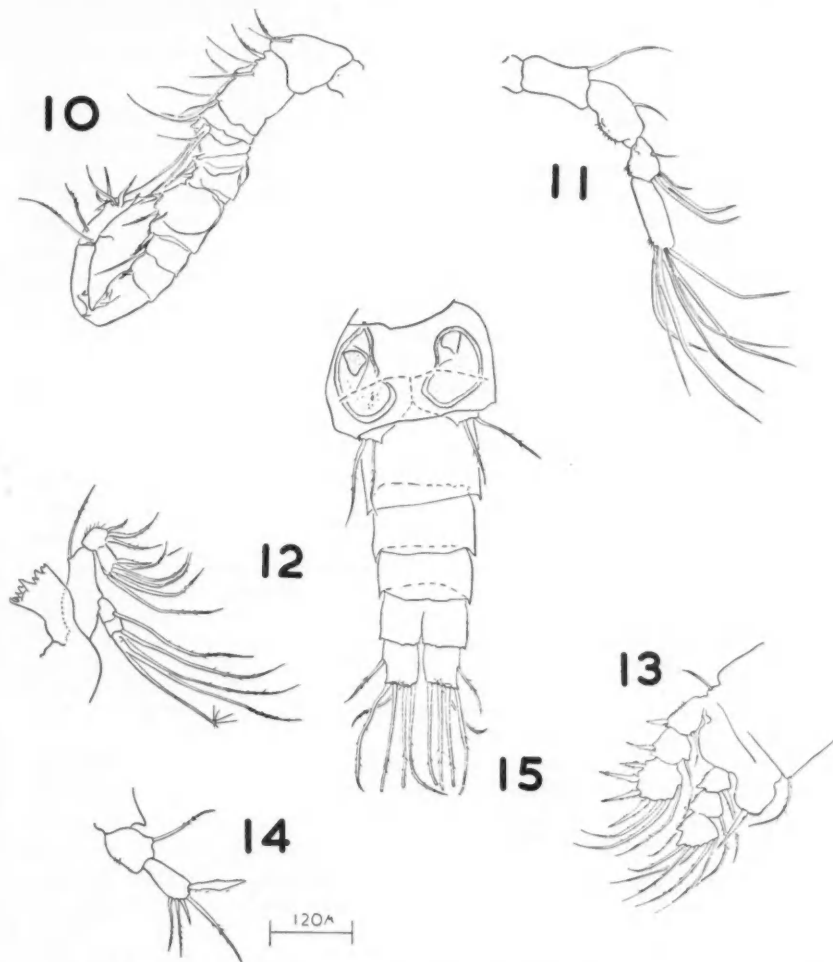
The fifth foot (Fig. 14) varies from that of the female in bearing five appendages on the terminal segment, rather than three: two spines and three setae. The terminal segment is more slender than that of the female. The urosome is five-segmented, with a vestigial pair of sixth legs on the genital segment, each of which bears two setae (Fig. 15). The caudal rami are little longer than wide, each with six plumose setae.

Specimens of *Cyclopina schneideri* male have been deposited at the British Museum (Natural History).

DISTRIBUTION IN THE UNGAVA BAY AREA. Members of this species were taken at four stations in 1947: 1, 3, 38 and 43. At station 43 they composed 50% of the total copepod population; the catch consisted of 78 females and 4 males.

At station 217, established in 1950 in Wakeham Bay, a haul was made at 4-8 feet in 10 feet of water near shore; here *C. schneideri* composed 70.5% of the copepod population. Less than 1% were counted in a subsample from station 222 at Lake Harbour, towing at a depth of 1 metre.

GENERAL DISTRIBUTION. This distinctly littoral species has been hitherto reported only from Vadsö Sound, East Finmark (Scott, 1903).



FIGURES 10-15. *Cyclopina schneideri* Scott ♂: 10. Antennule. 11. Antenna. 12. Mandible. 13. First swimming leg. 14. Fifth leg. 15. Urosome, ventral view.

Family MONSTRILLIDAE

Genus *Monstrilla* Dana*Monstrilla dubia* Scott

Monstrilla dubia Scott 1904, p. 247, pl. XIII, fig. 14, pl. XIV, figs. 16-18.

Monstrillopsis dubia Sars 1921, pp. 26-27, pl. XIV.

Monstrilla dubia Davis 1949, in key.

Davis (1949) in a revision of the Monstrilloidea has shown that there are only two valid genera of the sub-order, *Monstrilla* and *Thaumaleus*, and has renamed Scott's specimen *Monstrilla dubia*.

DISTRIBUTION IN THE UNGAVA BAY AREA. One male specimen was found at each of the following stations: station 9, hauling at 15-17 metres; station 3, at 6-7 metres; station 1 (July 20), at 12-14 metres and station 33, hauling at 10-13 metres. One female was taken at each of the following stations: station 7, at 6 metres; station 22, 2-1 metres; station 37, at the surface and station 51, at the surface.

GENERAL DISTRIBUTION. This is a North Atlantic form, previously reported from Norwegian waters (Sars, 1921) and from the coast of Scotland (Scott, 1904), but never before from the American side of the Atlantic, nor from arctic waters.

Monstrilla helgolandica Claus

Monstrilla helgolandica Claus 1863, p. 165, pl. 12, fig. 9; Sars 1921, pl. IX, p. 18.

DISTRIBUTION IN THE UNGAVA BAY AREA. One female of this species was taken at station 1, on the 20th of July, at 19-21 metres.

GENERAL DISTRIBUTION. This species has been recorded from Heligoland by Claus, from the Skagerak, from the North Sea and English Channel and from the Malay Archipelago by Scott (1909). The male is so far unknown, but Sewell (1949) who found females in the Indian Ocean, has proposed *M. serricornis* which was also present in his collections, and of which only males are known, as the male of the species. The distribution of *M. serricornis* corresponds with that of *M. helgolandica* (Norwegian coast, Indian Ocean). *M. helgolandica* has not previously been recorded from North American coasts, but males of *M. serricornis* were reported from the New England coast by Wilson (1932).

Monstrilla canadensis McMurrich

Monstrilla canadensis McMurrich 1917, p. 47.

DISTRIBUTION IN THE UNGAVA BAY AREA. Thirteen males of this species were captured at the following stations: five at station 7, at 5-6 metres, and two at the surface; five at station 9, at the surface and at 15-17 metres; one at station 3 at 6-7 metres.

GENERAL DISTRIBUTION. The first description was of males taken in Passamaquoddy Bay by McMurrich in 1917. The female is unknown, and this is apparently the farthest north that the species has penetrated.

DISCUSSION

Dunbar (1951) showed that the water masses of the eastern arctic of North America may be divided into five types by means of the temperature-salinity diagram. These five types are: (1) the Labrador Sea; (2) West Greenland water, consisting of a mixture of polar, Atlantic Drift (Irminger current), coastal and Labrador Sea water; (3) the Labrador current, running south along the Labrador shelf from Cape Chidley to the Newfoundland banks; (4) the deep water of Baffin Bay; (5) polar or arctic water (over all the region north of Davis Strait, and in Hudson Bay).

The water masses of Hudson Strait and Ungava Bay, and from the mouth of Hudson Strait and immediately outside, do not quite fit any of these five types. The water of Ungava Bay is warmer than the polar water of Hudson Bay; the surface salinities are higher, but are lower than those of West Greenland and the waters of the Labrador Sea. The warming is probably due to surface heating and vertical mixing, the low salinities to coastal drainage. The bulk of the Hudson Strait water probably comes from Hudson Bay. The water off the mouth of Hudson Strait is the point of origin of the Labrador current, where the Canadian current, the water from West Greenland and from Hudson Strait converge.

The low salinities of Hudson Bay, Hudson Strait and Ungava Bay do not indicate an invasion of West Greenland water (containing an Atlantic element) along with the water from Davis Strait (Canadian current), but certain biological aspects point strongly to such an invasion. Some of these biological considerations are: numbers of Atlantic cod (*Gadus callarias* Linnaeus) in the northeast part of Ungava Bay, near Port Burwell in the summer; the presence of *Hybocodon prolifer* L. Agassiz at Lake Harbour during the summer; the prevalence of this non-arctic species in Ungava Bay; the relative scarcity in Ungava Bay of *Themisto libellula*, which is usually the dominant species in arctic waters. These and other indicators are discussed fully by Dunbar (1951) as marking the Greenland waters, from Cape Farewell to Thule, the eastern part of Hudson Strait, together with Ungava Bay, as subarctic rather than arctic in nature.

Evidence based on the copepod distribution in Ungava Bay and adjacent waters also points to a subarctic type of water. Two individuals of a non-arctic species, *Pleuromamma robusta*, were found in the plankton from this area (at station 41). The specimens were accompanied by very small numbers of *Pareuchaeta norvegica*, *Gaidius tenuispinus* and *Heterorhabdus norvegicus*. The three latter species were also taken at station 103, along with *Aetideopsis rostrata*, represented by one individual. The scant numbers of these four species label them as "terminal immigrants", that is, individuals which can live in the conditions existing in Ungava Bay, but from which no new populations will be produced. They are arctic forms which have penetrated in small numbers southwards in the North Atlantic as far as the coast of New England. They are also known from West Greenland waters, both north and south of Davis Strait. Two specimens of *Pareuchaeta glacialis* were also taken from station 103, and it is interesting that this is as far west in Hudson Strait as the species is known to

occur, while *P. norvegica* has been found within the Bay at station 41. Other arctic forms, known from polar seas as well as from the North Atlantic, are *Metridia longa* and *Microcalanus pygmaeus*, both of which are well distributed throughout Ungava Bay. *Oncaea borealis*, of which adults, but few copepodites are known in Ungava Bay, is a surface-living species, common in the Arctic, and an inhabitant of American coasts down to Woods Hole.

The five most abundant species in Ungava Bay, *Calanus finmarchicus*, *C. hyperboreus*, *Pseudocalanus minutus*, *Oithona similis* and *Acartia longiremis*, are also both arctic and subarctic distribution. All of these are eurythermal but only three are euryhaline as well. The low salinity of the Bay would probably bar only the two species of *Calanus* from breeding, at least in the neritic regions, and this probably accounts for the paucity of *Calanus* in the southern-most stations of Ungava Bay. Jespersen (1939) found *Calanus finmarchicus* along the coast of East Greenland most plentiful in cold polar water close to the coast, which is of low mean salinity (29.58‰). However, even this measurement is higher than salinity at most of the stations (1, 3 and 7 are the only ones of which the salinities are known) in Ungava Bay where *Calanus* was scarce (Dunbar, 1951). Marshall, Nicholls and Orr (1935) showed that *Calanus* can adjust to salinities as low as 12–17‰ provided that the transition is a gradual one. Presumably the currents bringing in *Calanus* to Ungava Bay are swift enough to import them fairly suddenly to a new environment to which they cannot quickly adjust.

Calanus finmarchicus was most abundant at stations 18, 41 and 44 in 1947, stations 103, 123 and 128 in 1949, and at stations 223 and 234 in 1950. Maxima of *C. hyperboreus* were found at stations 18 and 41 in 1947, station 128 in 1949 and station 209 in 1950. All these stations are in approximately the northern half of the Bay, or in Hudson Strait. Station 18 was rich in *Calanus*, and stations 41 and 44 yielded tremendous quantities of the genus.

Pseudocalanus, known to be euryhaline and to breed in neritic regions in other parts of the world, for instance in the Gulf of Maine (Fish, 1936b), is plentiful everywhere in every stage of development throughout Ungava Bay. All stages of it were found in brackish water at station 51. In the southernmost part of the Bay, therefore, *Pseudocalanus* is prevalent, though it is accompanied and often replaced by *Oithona similis* and *Acartia longiremis*. The prevalence of these three species in the plankton of Ungava Bay, with a scarcity of *C. calanus*, forms a facies similar to that of Hudson Bay (Willey, 1931). Since the bulk of the Hudson Strait water is composed of outflow from Hudson Bay, and since a current from Hudson Strait, entering Ungava Bay at the northwest part of the Bay, flows south of Akpatok Island and out the northeast tip of the Bay, one would expect the plankton of the two basins to be highly similar. The great quantities of *Calanus* at stations 18, 41 and 44, together with the six species named above from stations 41, 44 and 103, can only be explained by an invasion of water from the eastern end of Hudson Strait, since these species probably do not come from Hudson Bay. The locations of stations 18 and 41, towards the southern end of the bay, indicate that this invading water flows well into the bay, probably entering the northwest part from the direction of Big Island, flowing across south of Akpatok Island and out

the northeast part of the bay. The presence of *Pleuromamma robusta* indicates that the inflowing water probably contains West Greenland water as well as polar water of the Canadian current from Davis Strait.

The *Godthaab* Expedition, 1928, investigated the waters west of Greenland from the Labrador Sea, north to Smith Sound (Jespersen, 1934). Jespersen divided the species of copepods found in this area into three groups: (1) species found in the whole of the investigated area; (2) species found exclusively or most often in the waters south of Davis Strait; (3) those usually found only in Baffin Bay and Davis Strait. Twenty-three species belong to the first group, and these include the 13 arctic and subarctic species of Ungava Bay. Seventy-six were put into the second group, and of these only *Pleuromamma robusta* occurs also in Ungava Bay. Finally, 13 were included in the last group, and of these only *Oncaea borealis* is also an inhabitant of Ungava Bay. (Its presence in the last group is doubtful, as it may have been missed by the stramin nets used south of Davis Strait.) Apparently, species which can withstand the low temperatures and salinities of Ungava Bay can penetrate the waters north of Davis Strait. Of the species found in the whole of the West Greenland area, the 13 which also occurred in Ungava Bay were taken in relatively shallow hauls by the *Godthaab* Expedition, usually with a 300-metre wire or shorter. The 12 remaining species which were absent in Ungava Bay were captured at the deeper stations of 294 metres, and usually deeper than that. Perhaps the 400-metre depth of Hudson Strait is too shallow for truly bathypelagic species to pass along.

The finding of *Acartia longiremis spiniremis* is in accordance with Pinhey's statement (1927) that all members of *Acartia longiremis* from the Atlantic and Pacific coasts of North America belong to this subspecies. Jespersen (1934) did not mention the subspecies as occurring in the West Greenland fauna, but the number of dissected specimens from Ungava Bay (16) was too small to be sure that *Acartia longiremis forma typica* does not also occur in this area.

The four species studied in detail have the same sort of life histories as they do in other parts of the world, in that adults of *Calanus* disappear at the end of August, whereas in the case of *Pseudocalanus*, *Oithona similis* and *Acartia longiremis*, adults and nauplii never disappear from the population. The annual life cycles determined for *Calanus* and *Pseudocalanus* are similar to the rate of development found for the two species in East Greenland waters (Digby, 1954). In East Greenland no second breeding period of *Calanus* was found to take place in the autumn. Perhaps the adult males and females which appear in Ungava Bay at stations 41 and 44 are Atlantic individuals brought in with *Pleuromamma robusta* and the accompanying species mentioned above.

Ungava Bay is too shallow, and the waters are too cold and of too low a salinity to accommodate the bathypelagic subarctic copepods found in West Greenland waters. However, certain minor considerations such as the presence of adult males and a few semi-ripe females of *Calanus finmarchicus* at stations 41 and 44, as well as the two specimens of *Pleuromamma robusta* might possibly point to a West Greenland contribution to the invading water at the eastern end of Hudson Strait.

SPECIES OF COPEPODA OCCURRING IN UNGAVA BAY AND CENTRAL HUDSON STRAIT

<i>Calanus finmarchicus</i> (Gunner)	<i>Pleuromamma robusta</i> (Dahl)
<i>Calanus helgolandicus</i> (Claus)	<i>Heterorhabdus norvegicus</i> (Boeck)
<i>Calanus hyperboreus</i> Krøyer	<i>Acartia longiremis</i> (Lilljeborg)
<i>Pseudocalanus minutus</i> Krøyer	<i>Acartia biflosa</i> (Giesbrecht)
<i>Microcalanus pygmaeus</i> (G. O. Sars)	<i>Oithona similis</i> Claus
<i>Gaidius tenuispinus</i> (G. O. Sars)	<i>Oncaea borealis</i> G. O. Sars
<i>Acteopsis rostrata</i> G. O. Sars	<i>Cyclopina gracilis</i> Claus
<i>Pareuchaeta norvegica</i> (Boeck)	<i>Cyclopina schneideri</i> Scott
<i>Pareuchaeta glacialis</i> (H. J. Hansen)	<i>Monstrilla dubia</i> Scott
<i>Eurytemora americana</i> Williams	<i>Monstrilla helgolandica</i> Claus
<i>Metridia longa</i> (Lubbock)	<i>Monstrilla canadensis</i> McMurrich

SUMMARY

Summer collections were made of the copepods of Ungava Bay and central Hudson Strait during late June, July and August of 1947, 1949 and 1950. The samples were taken in horizontal tows with fine-mesh nets (No. 18, No. 5 and No. 6) and with coarse-mesh nets (No. 0 and stramin).

Of the 22 species occurring in this area, two are littoral and brackish water forms *Eurytemora americana* and *Acartia biflosa*; two are littoral and marine forms *Cyclopina gracilis* and *C. schneideri*; the three species of *Monstrilla* are semi-parasitic.

Monstrilla dubia, *M. helgolandica*, *Cyclopina gracilis* and *C. schneideri* have not previously been reported from the American side of the North Atlantic. Males of *Cyclopina schneideri* are described for the first time.

Only one non-arctic species was taken in the entire collection and this (*Pleuromamma robusta*) was represented by only two individuals. The 14 remaining species (exclusive of *Calanus helgolandicus*) have been found in the waters west of Greenland, both north and south of Davis Strait. Probably Ungava Bay and Hudson Bay are too shallow, and the waters are too cold and of too low a salinity to permit the immigration of bathypelagic species from West Greenland and the North Atlantic.

Investigations were carried out on the life histories of the two most abundant species, *Calanus finmarchicus* and *Pseudocalanus minutus*. Both these species have annual life cycles, but breeding is to some extent continuous during the summer in the case of *Pseudocalanus* and a small part of the population of this species develops quickly enough to breed a second time at the end of August or the first week in September. There is little evidence for a second breeding period in the case of *Calanus* as most of the adults disappear by the end of August.

Brief studies were made of the life histories of *Acartia longiremis* and *Oithona similis*. The development of these species is similar to that of *Pseudocalanus* in that adult males never disappear from the population during the

summer. The spawning of *Acartia* may occur about the middle of July, as males and females are in abundance at that time and nauplii and small copepodites appear during the middle of August. The outline of the life history of *Oithona similis* is not so clearly defined, but the period of most active breeding evidently takes place in the first week of July. The products of this breeding peak appear as nauplii in mid-July, and nauplii and copepodites in mid-August.

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Echinoderms of Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound¹

"CALANUS" SERIES, NO. 9

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ABSTRACT

A collection of 26 species of echinoderms, collected between 1947 and 1952 by the *Calanus* expeditions in Ungava Bay, eastern Hudson Strait, Frobisher Bay and Cumberland Sound, is described. Included are one crinoid, 10 asteroids, 9 ophiurans, one echinoid and 5 holothurians; of which 6 asteroids, 5 ophiurans and 4 holothurians are new records for the collection areas.

INTRODUCTION

BETWEEN 1947 and 1952 about 1,200 specimens of echinoderms were collected by the *Calanus* expeditions in Ungava Bay, eastern Hudson Strait, Frobisher Bay and Cumberland Sound, in the eastern Canadian arctic. All 5 classes of the phylum are represented, and 26 species are included in the collection.

Since Sabine's (1824) account of the marine invertebrate animals collected by Parry's 1819-20 expedition at Melville Island, in the western Canadian arctic, about 45 species of echinoderms have been recorded from northern Canada, between southern Labrador and Alaska. Previous to the work of the *Calanus* only a few small collections of echinoderms had been made in the areas covered by these investigations, and 11 species had been recorded by the following authors: Verrill (1879), Cumberland Sound; Whiteaves (1884), Port Burwell; Pfeffer (1886), Cumberland Sound; Grieg (1893), Cumberland Sound; Clark (1920), Port Burwell and Hudson Strait; and Clark (1936), Hudson Strait.

The following 15 species are new records for the areas of the *Calanus* collection: *Ctenodiscus crispatus*, *Pteraster militaris*, *Lophaster furcifer*, *Solaster papposus*, *Henricia eschrichti eschrichti*, *Urasterias lincki*, *Gorgonocephalus arcticus*, *Ophiacantha bidentata*, *Ophiopus arcticus*, *Amphiura sundevalli*, *Ophiocten sericeum*, *Thyonidium* sp., *Cucumaria japonica*, *Cucumaria calcigera* and *Myriotrochus rinki*. Eleven species, reported here, have been recorded formerly from the collection areas: *Heliometra glacialis*, *Solaster endeca*, *Stephanasterias albula*, *Leptasterias groenlandica*, *Asterias polaris*, *Ophiopholis aculeata*, *Ophiura sarsi*, *Ophiura robusta*, *Stegophiura nodosa*, *Strongylocentrotus droebachiensis* and *Cucumaria fabricii*. Only two species known formerly from these areas were not present in the *Calanus* collection. They are *Leptasterias mülleri* (M. Sars)

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from Cumberland Sound (Verrill, 1879) and *Leptasterias littoralis* (Stimpson) from Ungava Bay (Whiteaves, 1884).

In the following account of the species, station numbers and the numbers of specimens taken at each station are given. The locations and depths of the collections may be found in the station lists of the *Calanus* expeditions (Dunbar and Grainger, 1952; Grainger, 1954). Northern Canadian records include all those found with reference to the area between southernmost Labrador and Alaska. The terms "arctic", "subarctic" and "boreal" are used as defined by Dunbar (1953).

SYSTEMATIC ACCOUNT OF THE SPECIES

Class Crinoidea

Family ANTEDONIDAE

Heliometra glacialis (Leach)

Recorded from as far west as Hudson Bay in North America, it extends eastward in the arctic and subarctic at least to the Siberian Sea. Northern Canadian records are from eastern Ellesmere Island (Duncan and Sladen, 1881, *Antedon eschrichtii*), northern Baffin Island (Rodger, 1894, *A. eschrichtii*), southern Ellesmere Island (Grieg, 1907, *A. eschrichtii*), Hudson Bay (Clark, 1922), Jones and Exeter Sounds (Mortensen, 1932), Hudson Strait, Foxe Basin, Cobourgh Island (Clark, 1936), Hudson Bay (Clark, 1936, 1937).

Calanus collection: 24 specimens, 77 to 192 metres. Stations 102 (1), 103 (11), 106 (1), 222 (5), 319 (1), 322 (1), 331 (1), 333 (1), 334 (2).

Class Asteroidea

Family PORCELLANASTERIDAE

Ctenodiscus crispatus (Retzius)

This is a circumpolar species, of arctic, subarctic and boreal waters. Northern Canadian records are from Melville Island (Sabine, 1824, *Asterias polaris*), Cornwallis Island (Forbes, 1852, *C. polaris*), Dolphin and Union Strait (Clark, 1920), Jones Sound (Mortensen, 1932), Hudson Bay (Clark, 1937).

Calanus collection: 1 specimen, 80 to 100 metres, station 201.

This 5-rayed specimen is large, with a diameter of 70 mm. and the ratio of the arm radius to the disc radius (R:r) 2.1:1. The width of the rays at the base reaches 22 mm. The abactinal paxillae, composed of about 7 to 19 spines, are largest midway along the rays. The madreporite measures 4 mm. across its widest part. On most of the adambulacral plates there are 3 large spines bordering the groove.

Family PTERASTERIDAE

Pteraster militaris (O. F. Müller)

This is probably a circumpolar species, of the arctic, subarctic and boreal regions. Northern Canadian records are from eastern Ellesmere Island (Duncan and Sladen, 1881), Jones Sound (Grieg, 1907), Foxe Basin (Clark, 1936), Hudson Bay (Clark, 1937).

Calanus collection: 2 specimens, 10 to 91 metres, stations 126 and 413.

The specimen from station 126 is particularly large, 105 mm. in diameter, with R:r equalling 2.3:1. There are 5 rays. The other specimen, from station 413, although 6-rayed, shows such close agreement in all other aspects with normal 5-rayed specimens of the species that it must be referred to this species. The diameter is 41 mm., and R:r equals 1.8:1. The 6 rays taper to slender, almost pointed tips. Many small calcareous deposits occur in the supra-abactinal membrane, and numerous spiracula are evident on the rays. The bases of the paxillae are low, and from these there extend 3 to 4 fairly long, slender spines, which support the supra-abactinal membrane. The adambulacral plates carry 7 transverse webbed spines proximally on the rays, the innermost one or two of these spines being considerably smaller than the others, all of which are joined by a web extending to near the outer margin of the actinolateral membrane. Each of the oral plates has 5 webbed spines, which decrease in size from the innermost laterally. The webs of adjacent oral plates are not joined. A single suboral spine occurs on each oral plate, being slightly longer and considerably thicker at the base than the innermost (largest) oral spine. This suboral spine, heavily sheathed, is clear distally, narrowing to an irregularly shaped tip.

Family SOLASTERIDAE

Lophaster furcifer (Düben and Koren)

This species is probably circumpolar, in arctic, subarctic and boreal waters. Northern Canadian records include eastern Ellesmere Island (Duncan and Sladen, 1881), southern Ellesmere Island (Grieg, 1907, *Solaster furcifer*), Hudson Bay (Clark, 1937).

Calanus collection: 1 specimen, 183 to 192 metres, station 334.

In this specimen the diameter is 100 mm., R:r = 2.8:1, and there are 5 rays. The abactinal paxillae have about 21 to 26 spines, each with 3 to 4 terminal points protruding as distal extensions of the lateral, longitudinal ridges of the spines. The ray width at the base is 21 mm. The adambulacral plates bear 3 to 4 spines parallel to the groove, and 3 to 5 spines in the transverse series.

Solaster papposus (L.)

A circumpolar species, it extends over the arctic, subarctic and boreal areas. Northern Canadian records are from Cornwallis Island (Forbes, 1852, *S. papposa*), Labrador (Packard, 1863, *S. papposa*; 1867, *Crossaster papposa*), eastern Ellesmere Island (Duncan and Sladen, 1881, *C. papposus*), Hudson Strait (Halkett, 1898), southern Ellesmere and northern Devon Island (Grieg, 1907), southern Ellesmere Island (Grieg, 1909), Dolphin and Union Strait, Somerset Island, Hudson Bay (Clark, 1920, *C. papposus*), Hudson Bay (Clark, 1922, *C. papposus*), Jones Sound (Mortensen, 1932), Foxe Channel, Foxe Basin, Melville Peninsula, Cobourg Island (Clark, 1936, *C. papposus*), Hudson Bay (Clark, 1937, *C. papposus*).

Calanus collection: 9 specimens, 18 to 145 metres. Stations 103 (2), 126 (1), 206 (1), 208 (1), 222 (2), 238 (1), 319 (1).

In these specimens the diameters are from 14 to 117 mm., and R:r = 1.8:1 to 2.2:1. There are 4 with 10 rays, 2 with 11 and 3 with 12. In the largest specimen (117 mm. diameter, 12 rays) there are 3 to 4 inner and 4 to 5 outer adambulacral spines, there are not more than 5 paxillae in any interradial area, and there are 9 marginal and 2 suboral spines on the oral plates. In the smaller specimens

(14 and 22 mm. diameter, 10 and 11 rays) there are 2 to 3 inner and 3 to 4 outer adambulacral spines, no interradiial paxillae are visible, and there are 7 marginal and 2 suboral spines on the oral plates.

Solaster endeca (L.)

This species is found from Somerset Island east to Novaya Zemlya, and in the eastern part of the North Pacific. Mortensen (1932) characterizes it as being a North Atlantic and North Pacific form, referring to its apparent absence from intermediate high arctic areas (North Greenland and the Siberian Sea). In view of this, Clark's (1920) record of it from presumably arctic Somerset Island in the Canadian arctic archipelago is of interest. It is apparently chiefly subarctic and boreal, but evidently extends into the arctic. Northern Canadian records are from Somerset Island (Walker, 1862), Labrador (Packard, 1867), Somerset Island, Hudson Strait (Clark, 1920), Hudson Bay (Clark, 1937).

Calanus collection: 4 specimens, 80 to 140 metres, Stations 103 (1), 201C (1), 319 (2).

In these specimens the diameter ranges from 15 to 150 mm., R:r from 1.7:1 to 2.7:1. In 3 individuals there are 9 rays, in one 10 rays. Following are measurements and spine counts of these specimens.

Diameter	R:r	Rays	Inner adambulacrals	Outer adambulacrals	Abactinal paxillae spines
150	2.7:1	9	-3	-7	c. 20-30
47	2.5:1	10	1-2	4-6	c. 3-9
40	2.1:1	9	1-2	4-5	c. 5-9
15	1.7:1	9	...	3-4	c. 4-9

In these specimens the adambulacral spines are most numerous nearest the base of the rays. There is an apparent increase in R:r and in the numbers of adambulacral and abactinal spines with increase in the size of the individuals.

Family ECHINASTERIDAE

Henricia eschrichti eschrichti (Müller and Troschel)

Heding (1935) re-examined specimens of the North Atlantic *Henricia sanguinolenta* group, and separated it into several distinct species, one of which is *Henricia eschrichti eschrichti*, recorded here. Acceptance of this work means a great restriction in the range of *H. sanguinolenta* (O. F. Müller), and a necessary re-examination of specimens from outside the area covered by Heding, in order to determine to which of the *sanguinolenta*-like species (or subspecies) the specimens previously recorded as *H. sanguinolenta* belong. While records previous to Heding's work indicate the distribution of *sanguinolenta* to extend widely over the North Atlantic area and to include also the North Pacific, Heding's findings appear to restrict *sanguinolenta* (at least within the Atlantic area bounded on the west by West Greenland) to the eastern Atlantic, and indicate that *eschrichti eschrichti* is the common West Greenland form, where also *eschrichti laevior* (Michailovskij) and *scabrior* (M.) are found. In view of this it is of considerable interest that all the *Calanus* specimens of this genus are *eschrichti eschrichti*, showing that this form extends into Canadian waters.

All other records of this genus from northern Canada and eastern North America refer to *Henricia sanguinolenta*. Whether these specimens are the true *sanguinolenta* or one or more of the *sanguinolenta*-like forms cannot be stated at present. The records are from Labrador (Packard, 1863, 1867, *Cribella oculata*; Bush, 1884, *C. sanguinolenta*), Foxe Basin (Clark, 1936), Hudson Bay (Clark, 1937).

Calanus collection: 21 specimens, 20 to 145 metres. Stations 13 (1), 30 (2), 33 (6), 58 (3), 103 (1), 106 (1), 126 (2), 208 (1), 226 (2), 317 (1), 319 (1).

While there is considerable variation within this small number of specimens, there appears to be good cause to place them all within *eschrichi eschrichi*. In all there are 5 rays, and R:r equals 2.9:1 to 4.0:1. Adambulacral, actinolateral, inferomarginal, intermarginal (restricted to the proximal part of the ray) and superomarginal plates are in regular imbricated rows (Fig. 1), while the remaining ray plates, including the carinals, are irregularly reticulate (Fig. 2).

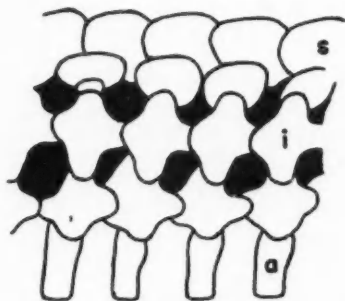


FIGURE 1. Lateral ray plates of *Henricia eschrichi eschrichi*. Superomarginals (s), inferomarginals (i), adambulacral (a).

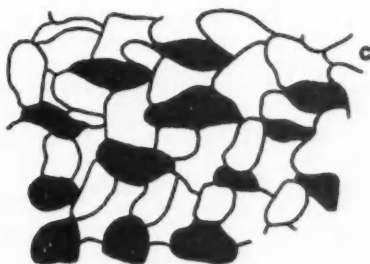


FIGURE 2. Abactinal ray plates of *Henricia eschrichi eschrichi*. Carinals (c).

Single papulae occur between the actinolaterals and inferomarginals, and between the inferomarginals and intermarginals (or superomarginals). The abactinal spines number from about 4 to 35 per paxilla, and the adambulacral spines from 7 to 17 (excluding the small single spine set well down in the groove). In both of these counts somewhat higher numbers are found than are given by Heding, who reported "pseudopaxillae bristly with 8 to 20 spines in each. Adambulacral with few (about 10) spines". Data are given on 18 specimens below.

Diameter (mm.)	R: r	Adambulacral spines	Actinolateral paxillae spines	Abactinal paxillae spines (approximate counts)
47	3.7: 1	14-17	14-16	12-35
40	3.3: 1	14-17	12-13	20-30
39	3.1: 1	10-12	12-13	7-20
39	4.0: 1	13-15	11-15	11-20
38	3.6: 1	8-10	6-9	4-12
35	2.9: 1	10-13	...	7-30
34	3.2: 1	7-10	7-8	6-16
32	3.4: 1	11-13	7-9	7-18
30	3.0: 1	12-13	9-13	11-20
27	3.8: 1	15-16	12-14	12-35
26	4.0: 1	8	7-9	9-12
25	2.9: 1	10-12	7-10	8-10
24	4.0: 1	7-9	6-9	5-10
24	3.3: 1	8-9	5-6	4-9
23	3.7: 1	10-12	7-9	9-20
21	3.0: 1	7-8	5-6	7-20
18	3.7: 1	9-11	...	9-20
17	3.0: 1	8-10	5-6	10-20

The wide range in the last 3 columns above is notable. Little correlation can be seen between diameter and R:r measurements, or between the sizes of the individuals and the spine counts, although high spine counts in one part generally are accompanied by high counts in other parts of the same individual. Figure 3 shows adambulacral and actinolateral spines from 2 specimens. On the left (1) is a 26-mm. specimen ($R:r = 4.0:1$) in which there are 8 adambulacral and 6 actinolateral spines, the former in 2 distinct rows. On the right (2) is a 47-mm. specimen ($R:r = 3.7:1$) showing 14 (plus the single groove spine) adambulacral and 15 actinolateral spines. In this the 2-row pattern in the innermost adambulacral spines is somewhat obscured.

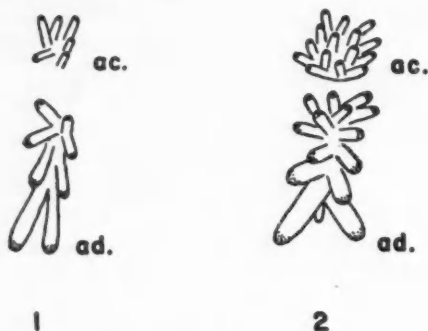


FIGURE 3. Adambulacral (ad) and actinolateral (ac) spines of 2 specimens of *Henricia eschrichti eschrichti*.

Family ASTERIDAE

Stephanasterias albula (Stimpson)

This species apparently is limited principally to the arctic and subarctic regions, extending from Melville Peninsula east at least to the Kara Sea. Fisher (1930) reported it from the North Pacific, but Mortensen (1932) doubted its presence in the Pacific area. Shorygin (1948) reported it from the Bering Sea, probably on the strength of Fisher's report. Northern Canadian records are from Cumberland Sound (Verrill, 1879), eastern Ellesmere Island (Duncan and Sladen, 1881, *Stichaster albulus*), southern Ellesmere Island and northern Devon Island (Grieg, 1907, 1909, *Stichaster albulus*), Burwell (Clark, 1920), Jones Sound (Mortensen, 1932), Foxe Basin, Melville Peninsula, Cobourg Island (Clark, 1936).

Calanus collection: 39 specimens, 10 to 145 metres. Stations 58 (1), 103 (1), 225 (3), 317 (3), 318 (1), 319 (6), 402 (5), 406 (6), 413 (3), 418 (10). Diameters extend from 7 to 42 mm., and the number of rays varies from 3 to 7, with more than 75% of the individuals having 6 rays.

Urasterias lincki (Müller and Troschel)

The known distribution of this predominantly arctic and subarctic species is from Dolphin and Union Strait east to the New Siberian Islands. It has not been recorded from the Bering Sea or the North Pacific. Northern Canadian records are from Dolphin and Union Strait (Clark, 1920) and Hudson Bay (Clark, 1920, 1922, 1937).

Calanus collection: 2 specimens, 80 metres, station 201C. Diameters are 145 and 295 mm., and the R:r values are respectively 5.2:1 and 7.4:1.

Asterias polaris (Müller and Troschel)

This species is found in the North Pacific and the Bering Sea, and in the Atlantic area, east only to West Greenland and south to New England. It is apparently unknown from East Greenland east to the Siberian Sea. Northern Canadian records are from Labrador (Packard, 1863, *Asteracanthion polaris*, 1867; Bush, 1884; Rankin, 1901), Burwell (Whiteaves, 1884), Cumberland Sound (Pfeffer, 1886), Burwell (Clark, 1920, *Asterias acervata borealis*), Hudson Bay (Clark, 1922, *A. acervata borealis*, 1936, 1937, *Leptasterias polaris*).

Calanus collection: 18 specimens, 0 to 110 metres. Stations 18 (1), 40 (1), 106 (4), 126 (5), 208 (4), 210 (2), 318 (1). Diameters range from 61 to 240 mm., R:r from 3.8:1 to 5.0:1. All have 6 rays.

Leptasterias groenlandica (Steenstrup)

This circumpolar species is arctic and subarctic in distribution. Records from northern Canada are from Cornwallis Island (Forbes, 1852, *Uraster violacea*), Somerset Island (Walker, 1862, *U. violacea*), Labrador (Packard, 1867, *Asterias groenlandica*), Cumberland Sound (Verrill, 1879), eastern Ellesmere Island (Duncan and Sladen, 1881, *Asteracanthion groenlandicum*), Cumberland Sound (Pfeffer, 1886, *Asterias groenlandicum*), southern Ellesmere Island and northern Devon Island (Grieg, 1907, 1909, *Asterias mulleri groenlandica*), Bernard Harbour, Dolphin and Union Strait (Clark, 1920, *Ctenasterias cribraria*), Hudson Bay (Clark, 1922), Jones Sound (Mortensen, 1932), Hudson Strait, Cobourg Island (Clark, 1936).

Calanus collection: 65 specimens, 0 to 145 metres. Stations 3 (1), 13 (1), 20 & 21 (1), 33 (7), Burwell (2), 103 (1), 201C (2), 203 (7), 206 (1), 226 (19), 234 (1), 317 (2), 318 (1), 319 (1), 321 (3), 402 (2), 404 (6), 418 (5), Ogac Lake (1), stomach of Atlantic cod, *Gadus callarias*, Ogac Lake (1). While specimens of both of this species and *Asterias polaris* were taken in the same general regions, on no occasion were both taken at the same station.

Without exception these specimens show slender elongate areas between the abactinolateral plates of the rays, areas extending generally without interruption from the supermarginals to the carinals. Thus they appear to be of the *cribraria* form of this species. The carinals are variable, generally fairly irregularly placed plates. Spines are particularly abundant around the madreporite. The adambulacral spines are irregularly monacanthid and diplacanthid. The diameters range from 4 to 73 mm., R:r values from 2.0:1 to 5.0:1. There is evidently a general increase in the R:r value with increase in the size of the animal.

One specimen, taken from station 321, on August 8, 1951, held about 12 young (about 2 mm. in diameter) between its downward folded rays. There was no evidence of young within the stomach of this animal or within any of the others examined (as was demonstrated by Lieberkind, 1920). The smallest specimens taken, apart from the young above, were 4 mm. in diameter, and apparently were not accompanied by any larger individuals. These 4-mm. specimens resemble closely the 2-mm. young, from which similarity there is no doubt as to their identity. Abactinal and actinal views of a ray of one of these (R:r = 2.1:1) are shown in Figure 4. In the abactinal view (1) are shown the relatively large and conspicuous terminal plate bearing many large spines, the spine-bearing lateral marginal plates, and a lone circular plate in the centre of the abactinal face of the disc. There is no evidence of any abactinal ray plates. In the actinal view (2) are shown the long terminal ray spines, the adambu-

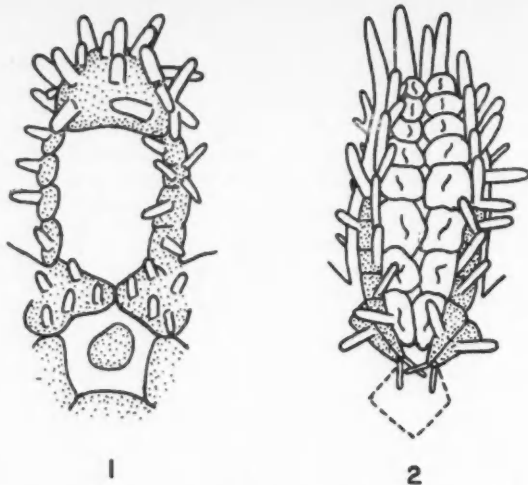


FIGURE 4. Ray of a 4-mm. diameter specimen of *Leptasterias groenlandica*, showing abactinal (1) and actinal (2) surfaces.

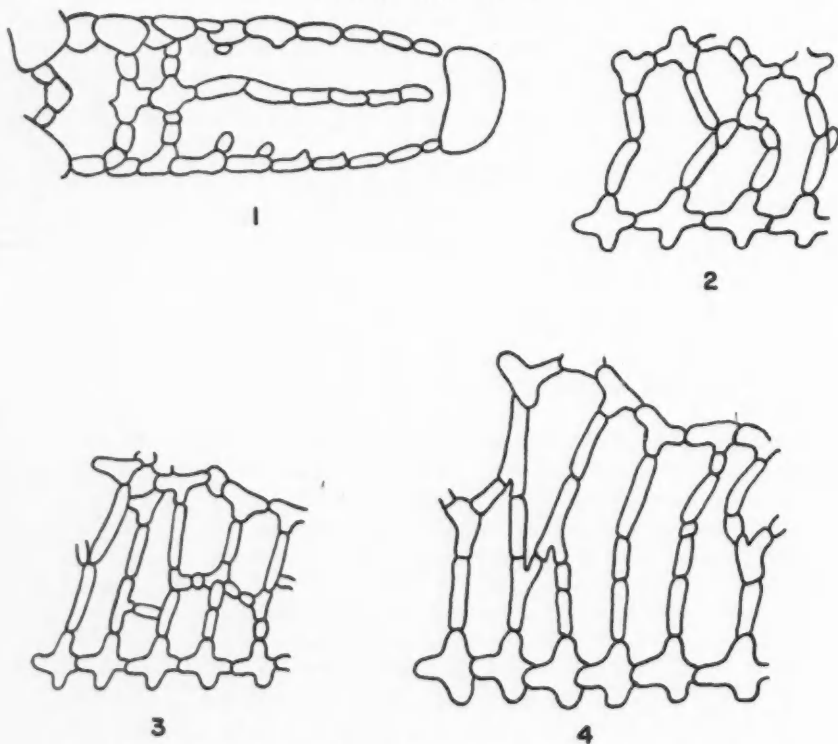


FIGURE 5. *Leptasterias groenlandica*. Abactinal view of ray plates of a 9-mm. specimen (1), and abactinolateral ray plates of a 25-mm. specimen (2), of a 38-mm. specimen (3), and of a 54-mm. specimen (4).

lacrals bearing irregularly one and 2 spines, as in larger specimens, and 2 distinct rows of tube feet. In Figure 5 is shown the abactinal plate arrangement in a 9-mm. specimen ($R:r = 3.1:1$), in which the terminal plates occupy relatively less of the ray, the carinals have formed a distinct row, much more regular than in larger specimens, and 2 transverse rows of abactinolateral plates have appeared. In the same figure further development of the abactinolateral plate arrangement is shown in specimens of 25, 38 and 54 mm. diameter.

Class Ophiuroidea

Family GORGONOCEPHALIDAE

Gorgonocephalus arcticus Leach

This species is recorded from Hudson Bay east to the Siberian Sea, in arctic and subarctic waters. It is not known from the Pacific or from the Bering Sea. Northern Canadian records are from Labrador (Grieg, 1893, *G. agassizii*), southern Ellesmere Island (Grieg, 1907), Hudson Bay (Clark, 1937).

Calanus collection: 34 specimens, 55 to 145 metres. Stations 102 (3), 103 (9), 106 (2), 126 (2), 206 (4), 210 (3), 226 (6), 231 (1), 319 (2), 333 (2). Disc diameters range from 8 to 65 mm.

Family OPHIACANTHIDAE

Ophiacantha bidentata (Retzius)

This circumpolar species ranges widely in arctic, subarctic and more southern waters. Its northern Canadian records are from Cornwallis Island (Forbes, 1852, *Ophiocoma echinulata*), Somerset Island (Walker, 1862, *Ophiura echinulata*), Labrador (Packard, 1863, 1867, *Ophiacantha spinulosa*), Prince Regent Inlet, northeastern Baffin Island, Labrador (Grieg, 1893), southern Ellesmere and northern Devon Island (Grieg, 1907), Hudson Bay (Clark, 1922), Jones and Exeter Sounds (Mortensen, 1932), Labrador, Foxe Channel, Foxe Basin, Melville Peninsula, Cobourg Island (Clark, 1936), Hudson Bay (Clark, 1937).

Calanus collection: 184 specimens, 15 to 274 metres. Stations 13 (1), 17 (1), 30 (2), 33 (81), 58 (10), 102 (8), 103 (8), 105 (1), 203 (1), 206 (1), 222 (1), 226 (3), 231 (4), 234 (3), 317 (18), 319 (11), 321 (1), 331 (3), 333 (12), 334 (2), 406 (11), 416 (1).

Disc diameters range from 3 to 14 mm., with the majority of specimens approximately 10 mm. In most specimens there is only one tentacle scale at the first pore on the rays, but in a few there are 2 scales per pore (as shown by Heding, 1935, fig. 25). In several, however, the pore scale number is variable within single specimens; in one individual, for example, there are 2 scales at one pore, and only one at each of the other 9. As has been found elsewhere, this character does not seem to be a valid one for distinguishing varieties.

Family OPHIACANTHIDAE

Ophiopholis aculeata (L.)

This is probably a circumpolar species, although it has not yet been recorded between Hudson Bay and the Bering Sea. It occurs in arctic, subarctic and boreal waters. Northern Canadian records are from Labrador (Packard, 1863, *Ophiacantha aculeata*, 1867; Bush, 1884), Burwell (Whiteaves, 1884), eastern Ellesmere Island (Fewkes, 1888, indefinite identification), Labrador (Grieg, 1893, *Ophiopus aculeata*; Rankin, 1901), Hudson Bay and

Strait (Clark, 1920), Hudson Bay (Clark, 1922), Hudson Strait, Cobourg Island (Clark, 1936), Hudson Bay (Clark, 1937).

Calanus collection: 43 specimens, 18 to 145 metres. Stations 30 (1), 33 (1), 103 (8), 126 (2), 206 (3), 208 (6), 210 (5), 226 (16), 333 (1). Disc diameters range from 6 to 17 mm.

Ophiopus arcticus Ljungman

This arctic-subarctic species is recorded from Foxe Basin east to Spitzbergen. Northern Canadian records are from northeastern Baffin Island (Grieg, 1893), Jones and Exeter Sounds (Mortensen, 1932), Foxe Channel and Basin (Clark, 1936).

Calanus collection: 12 specimens, 27 to 183 metres. Stations 317 (8), 329 (4). Discs range from 4 to 7 mm. in diameter.

Family AMPHIURIDAE

Amphiura sundevalli (Müller and Troschel)

Circumpolar, this species is arctic and subarctic in distribution. Northern Canadian records are from Cornwallis Island (Forbes, 1852, *Ophiolepis filiformis*, uncertain identity), Labrador (Packard, 1867, *A. Holbölli*), eastern Ellesmere Island (Duncan and Sladen, 1881, *A. Holboelli*), Labrador (Bush, 1884), Prince Regent Inlet (Grieg, 1893), Jones and Exeter Sounds (Mortensen, 1932).

Calanus collections: 2 specimens, 27 and 274 metres. Stations 317 (1), 416 (1). The disc diameters are 5 and 9 mm.

Family OPHIOLEPIDAE

Ophiura sarsi Lütken

Probably circumpolar, this species is found in arctic, subarctic and boreal waters. Northern Canadian records are from Labrador (Packard, 1867, *Ophioglypha sarsi*), eastern Ellesmere Island (Duncan and Sladen, 1881, *Ophioglypha sarsi*), Burwell (Whiteaves, 1884, *Ophioglypha sarsi*), northeastern Baffin Island (Grieg, 1893, *Ophioglypha sarsi*), southern Ellesmere Island (Grieg, 1907), Burwell, Hudson Bay (Clark, 1920), Jones and Exeter Sounds (Mortensen, 1932), Cobourg Island (Clark, 1936), Hudson Bay (Clark, 1937).

Calanus collection: 24 specimens, 55 to 274 metres. Stations 102 (5), 107 (1), 222 (8), 231 (1), 319 (7), 416 (2).

Disc diameters range from 7 to 29 mm. There are 7 specimens between 7 and 12 mm., 16 between 18 and 25 mm., and one of 29 mm. diameter.

No specimens similar to Grieg's (1907) short-spined variety from Jones Sound occurred in the *Calanus* collection. In these the number of tentacle scales is variable. Generally there are 2 scales per pore in the central joints of the rays, but almost always more (many with 5, some with as many as 7) on the innermost pores. Often there is only one scale per pore on the distal parts of the rays. In the largest specimen (29 mm. diameter disc) a decapod crustacean at least 25 mm. long was found.

Ophiura robusta (Ayres)

Possibly circumpolar, this species is not yet recorded from the Siberian Sea. It extends over arctic, subarctic and boreal areas. Known northern Canadian distribution is Cornwallis Island (Forbes, 1852, *O. fasciculata*), Somerset Island (Walker, 1862, *O. fasciculata*), eastern Ellesmere Island (Duncan and Sladen, 1881, *Ophioglypha robusta*), Labrador (Bush, 1884, *Ophioglypha robusta*), Burwell (Whiteaves, 1884, *Ophioglypha robusta*), Prince Regent Inlet, northeastern Baffin Island, Cumberland Sound (Grieg, 1893, *Ophioglypha robusta*), southern

Ellesmere and northern Devon Island (Grieg, 1907), Dolphin and Union Strait, Melville Island, Hudson Bay (Clark, 1920, *Ophiozea robusta*), Hudson Bay (Clark, 1922, *Ophioglyphina robusta*), Jones and Exeter Sounds (Mortensen, 1932), Foxe Channel and Basin, Melville Peninsula, Cobourg Island (Clark, 1936), Hudson Bay (Clark, 1937).

Calanus collections: 79 specimens, 18 to 192 metres. Stations 30 (1), 33 (1), 102 (10), 103 (3), 106 (2), 208 (6), 210 (2), 222 (1), 225 (2), 231 (4), 317 (5), 318 (1), 319 (32), 321 (4), 334 (1), 406 (2), Ogac Lake (2, from the Atlantic cod, *Gadus callarias*).

Disc diameters range from 3 to 9 mm., falling well short of the maximum northern size of about 12 mm.

Stegophiura nodosa (Lütken)

This principally subarctic species has not been recorded between West Greenland and Spitzbergen. Northern Canadian records include Labrador (Packard, 1863, 1867, *Ophioglyphina nodosa*), Cumberland Sound (Verrill, 1879, *O. nodosa*), Labrador (Bush, 1884, *O. nodosa*), Burwell (Whiteaves, 1884, *O. nodosa*), Prince Regent Inlet, northern Baffin Island, Cumberland Sound (Grieg, 1893, *Ophiura nodosa*), Bernard Harbour, Burwell (Clark, 1920), Exeter Sound Mortensen, 1932), Melville Peninsula (Clark, 1936).

Calanus collection: 107 specimens, 18 to 130 metres. Stations 30 (1), 33 (23), 102 (4), 107 (2), 203 (12), 222 (1), 231 (10), 234 (47), 318 (5), 404 (2).

The discs range from 2 to 9 mm. in diameter. The number of arm spines is very variable in this collection, ranging from none to 5 per ray. Varying similarly are the tentacle scales of the ray pores. Shown below in tabular form are tentacle scale and spine variations in specimens of 2, 4, 6 and 8 mm. diameter. Tentacle scales are given as proximal to the pore (p) and distal to the pore (d).

Diameter	Number of tentacle scales per pore									Maximum number of spines
	1st p d	2nd p d	3rd p d	4th p d	5th p d	6th p d	7th p d	8th p d	terminal p d	
8 mm.	4 3	5 3	5 2	5 2	4 1	4 1	4 1	4 0	3 1	5
6 mm.	3 2	4 2	4 1	3 1	3 0	1 0	3
4 mm.	3 1	4 1	3 0	3 0	2 0	2 0	2 0	1 0	1 0	2
2 mm.	2 0	2 0	2 0	2 0	1 0	1 0	1 0	1 0	1 0	1

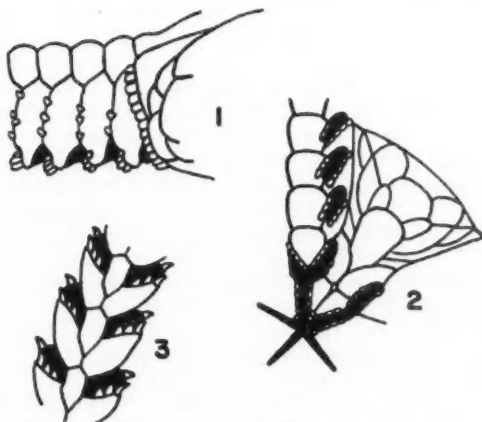


FIGURE 6. Lateral ray spines (1), proximal actinal pore scales (2), and distal actinal pore scales (3) of *Stegophiura nodosa*.

In Figure 6 (1) the spines on the proximal joints are shown in a lateral view of part of a ray of a 8-mm. specimen. In Figure 6 (2) are shown the tentacle scales of the proximal ray pores, and in Figure 6 (3) the distal tentacle scales of the same specimen.

Ophiocten sericeum (Forbes)

This species extends eastward from Dolphin and Union Strait to the Siberian Sea, and is not recorded from the North Pacific or the Bering Sea. It is arctic, subarctic and boreal. The northern Canadian records are from Cornwallis Island (Forbes, 1852, *Ophiura sericea*), eastern Ellesmere Island (Duncan and Sladen, 1881), Prince Regent Inlet, northeastern Baffin Island (Grieg, 1893), southern Ellesmere and Devon Island (Grieg, 1907), Dolphin and Union Strait, Melville Island, Hudson Bay (Clark, 1920), Hudson Bay (Clark, 1922), Jones and Exeter Sounds (Mortensen, 1932), Melville Peninsula, Cobourg Island (Clark, 1936), Hudson Bay (Clark, 1937), western Ellesmere Island (Vibe, 1950).

Calanus collection: 34 specimens, 80 to 274 metres. Stations 222 (3), 329 (30), 416 (1).

The disc diameters range from 12 to 18 mm. There is considerable variation in the shapes of the discs of these specimens, which vary from almost circular to distinctly pentagonal. Differences are found too in the spines on the distal margins of the upper ray plates, some having as many as 20 spines (2 groups of about 10 each on either side of the centre line) on the proximal joints, others having none. Of 30 specimens, 17 bore these spines and 13 did not. The transverse striae on the lateral ray plates referred to by Mortensen (1933) are conspicuous in these specimens.

Class Echinoidea

Family STRONGYLOCENTROTIDAE

Strongylocentrotus droebachiensis (O. F. Müller)

This is a widely distributed circumpolar species, found in arctic, subarctic and more southern regions. Northern Canadian records are many, and are from Cornwallis Island (Forbes, 1852, *Echinus neglectus*), Somerset Island (Walker, 1862, *E. neglectus*), Labrador (Packard, 1863, *Fozopneustes droebachiensis*, 1867, *Euryechinus droebachiensis*), Hudson Bay, Labrador (Agassiz, 1865, *Echinus granularis*), Cumberland Sound (Verrill, 1879), eastern Ellesmere Island (Duncan and Sladen, 1881), Labrador (Bush, 1884), Burwell (Whiteaves, 1884), Cumberland Sound (Pfeffer, 1886), northeast Baffin Island (Rodger, 1894), Hudson Strait, Ungava Bay (Halkett, 1898), Labrador, eastern Ellesmere Island (Rankin, 1901), southern Ellesmere and northern Devon Islands (Grieg, 1907), Somerset Island, Hudson Bay, Melville Island, Bernard Harbour, Dolphin and Union Strait, Coronation Gulf (Clark, 1920), Hudson Bay (Clark, 1922), Jones and Exeter Sounds (Mortensen, 1932), southern Southampton Island (Brooks, 1935), Labrador, Hudson Strait, Foxe Basin, Frozen Strait, Cobourg Island (Clark, 1936), Hudson Bay (Clark, 1937), western Ellesmere Island (Vibe, 1950).

Calanus collection: 448 specimens, 5 to 192 metres. Stations 18 (1), 58 (1), 102 (1), 103 (3), 106 (9), 126 (1), 206 (1), 208 (4), 210 (4), 222 (4), 226 (2), 318 (1), 319 (6), 322 (2), 333 (7), 334 (7), 406 (5), 417 (2), Ogac Lake (387, including 379 from Atlantic cod stomachs, *Gadus callarias*). In these specimens diameters range from 4 to 70 mm., and ratio of height to diameter from 1:15 to 1:2.2.

Class **Holothurioidea**Family **PHYLLOPHORIDAE***?Thyonidium* sp.

About 130 specimens of probable representatives of this genus were collected by the *Calanus*, all originating from the stomachs of seals, walrus and cod. Unfortunately none of the specimens was in a suitable state of preservation to permit identification; in none were any spicules visible, and in only a few was it possible to examine tentacle structure. The largest specimens reached a length of about 15 cm. and a width of about 2 cm. Troschel's (1846) record of *Orcula Barthii* (*Thyonidium barthi*) from Labrador is the most northern previous record found for this genus from northeastern Canada.

Calanus collection: Burwell region of Ungava Bay (about 70, from stomachs of the Atlantic cod, *Gadus callarias*), off the mouth of the Koksoak River, off the Gyrfalcon Islands, and off the mouth of the Payne River, Ungava Bay (about 59, from stomachs of the square flipper seal, *Erignathus barbatus*), off Loksland, southeastern Frobisher Bay (about 3, from the stomach of a walrus, *Odobenus rosmarus*).

Family **CUCUMARIIDAE***Cucumaria japonica* Semper

Recorded formerly from the North Pacific, *japonica* was found in West Greenland and in Jones Sound by Mortensen (1932), who suggested the possibility of continuous distribution of this form from the Pacific east to Greenland. Following Mortensen's discovery of this form from West Greenland, he re-examined other Greenland specimens recorded originally as *frondosa*, and found them generally to be of the *japonica* type. It was then noted that the true *frondosa* occupied the northeast Atlantic region and extended northwest as far as Davis Strait, in which region it appeared to be replaced largely by *japonica*. According to Mortensen, "the finding of *Cuc. japonica* in the Greenland seas makes it rather certain that this species—or variety—is distributed also over the Arctic Sea to the north of America and the Bering Sea". This has a great bearing on the identity of the *Cucumaria* specimens of northern North America, where, of the 2 species above, only *frondosa* (apart from Mortensen's findings) is recorded, as one of the most frequently found echinoderms in the area. Following Mortensen's work, Grieg, who had reported *frondosa* from southern Ellesmere and northern Devon Island in 1907 and 1909, re-examined his specimens and found that they agreed with Mortensen's findings, and were *japonica* (Mortensen, 1932).

Following are the other northern Canadian records of *C. frondosa*: Cornwallis Island (Forbes, 1852, *C. fucicola*), Labrador (Packard, 1863, 1867, *Pentacta frondosa*), Burwell (Whiteaves, 1884, *P. frondosa*), Hudson Strait (Halkett, 1898, *P. frondosa*), Somerset Island, Hudson Bay (Clark, 1920), Hudson Bay (Clark, 1922, 1937). According to Mortensen's conclusions, many, or perhaps all of these are really *japonica*, a matter which can be decided only by a re-examination of the specimens.

Calanus collection: 10 specimens, 18 to 73 metres. Stations 11 (1), 58 (5), 107 (1), 203 (1), 238 (1), 317 (1). The following records are of specimens too badly preserved to permit identification beyond genus: off the Gyrfalcon Islands, Ungava Bay (5, from stomachs of the square-flipper seal, *Erignathus barbatus*), 202 (about 15, from the stomach of a square-flipper seal).

Cucumaria frondosa specimens from St. Andrews, N.B., were compared with the *Cucumaria* of the *Calanus* collection, and the visible differences between them were found to be limited to the spicules. Tube feet and body wall spicules from a 50-mm. long *frondosa* from St. Andrews are shown in Figure 7. Except

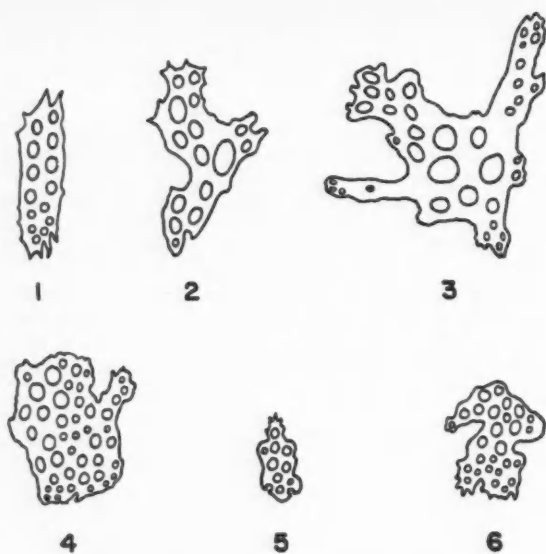


FIGURE 7. Tube feet spicules (1-3) and terminal body wall spicules (4-6) of *Cucumaria frondosa*.

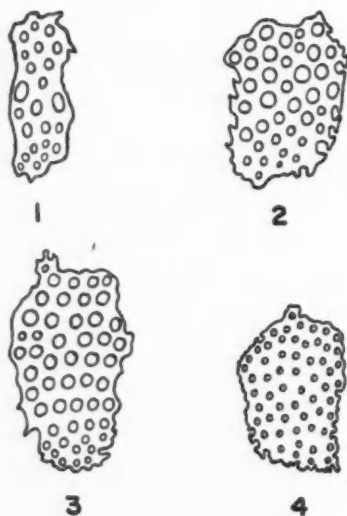


FIGURE 8. Body wall spicules (1-2) and tube feet spicules (3-4) of *Cucumaria japonica*.

for the smallest deposits (1), they tend to be irregular in outline with the openings placed unevenly and of various size. The body wall spicules are sparsely distributed, except terminally. In Figure 8 are shown spicules from *japonica*. These are clearly more rectangular in outline, and the perforations are generally more regularly arranged, often in readily discernible rows, and are nearer to one size, than in *frondosa*. In the larger spicules the openings at one end are smaller than elsewhere in the spicule, and the portion of the structure is thicker, with a more ragged outline and surface than is seen in the remainder of the spicule.

As these findings agree closely with Mortensen's discoveries in West Greenland, the *Calanus* specimens must be classed as *japonica*, rather than be identified as true *frondosa*. *C. japonica* is considered here, tentatively, as being a separate species, as was proposed by Semper (1868). Mortensen (1932) referred to this form as both *C. frondosa japonica* and *C. japonica*, and expressed uncertainty as to whether it should be considered as being a subspecific form of *C. frondosa* or as a separate species.

Cucumaria calcigera (Stimpson)

This species is recorded from Cornwallis Island east to West Greenland, and in the Kara Sea, Bering Strait and North Pacific. Its distribution is chiefly subarctic. Northern Canadian records are from Cornwallis Island (Forbes, 1852, *C. Hyndmanni*), Labrador (Packard, 1863, 1867, *Pentacta calcigera*; Bush, 1884, *P. calcigera*), Hudson Bay (Clark, 1920, 1922).

Calanus collection: 1 specimen, 27 to 37 metres, station 45. This specimen is about 60 mm. long, with plates spread conspicuously over the surface, and the tapering caudal end about one third the entire length of the animal.

Family PSOLIDAE

Psolus fabricii (Düben and Koren)

This species is probably circumpolar, although it is not yet recorded from Canada west of Hudson Bay. It is arctic and subarctic. Northern Canadian records are from Labrador (Packard, 1863, 1867, *Lophothuria fabricii*; Bush, 1884, *L. fabricii*, southern Ellesmere Island (Grieg, 1907, 1909), Burwell, Hudson Strait and Bay (Clark, 1920, *L. fabricii*), Hudson Bay (Clark, 1937).

Calanus collection: 37 specimens, 15 to 110 metres. Stations 45 (12), 55 (1), 58 (5), 59 (2), 106 (1), 126 (2), 203 (2), 210 (2), 226 (3), 238 (4), 317 (1), 406 (2). These range in length from about 8 to about 100 mm.

Family SYNAPTIDAE

Myriotrochus rinki Steenstrup

This is a circumpolar, arctic and subarctic species. Northern Canadian records are from Cornwallis Island (Huxley, 1852, *Chiridota brevis*), Labrador (Packard, 1867), southern Ellesmere Island (Grieg, 1907, 1909), Bernard Harbour, Dolphin and Union Strait (Clark, 1920), Exeter Sound (Mortensen, 1932), Hudson Bay (Clark, 1937).

Calanus collection: 62 specimens, 30 to 183 metres. Stations 102 (14), 107 (4), 201C (11), 203 (6), 234 (15), 329 (12). Six additional specimens were collected in 1953 by D. V. Ellis in upper Frobisher Bay at a depth of about 4 metres. Their lengths (exclusive of tentacles) ranged from 7 to 29 mm.

ZOOGEOGRAPHICAL REMARKS

Of 24 of the 26 species recorded here (*Henricia eschrichti eschrichti* and *Thyonidium* are not included), 14 species (58%) are circumpolar or probably so.

While 18 (75%) of the 24 species are recorded also from the North Pacific, all but two are found widely throughout the North Atlantic area. These two exceptions show interesting and possibly similar distributions. *Asterias polaris* occurs in the North Pacific and also in the North Atlantic area only as far east as West Greenland. It is probable that it extends across the intermediate area of northern Canada. Also *Cucumaria japonica* is known from the North Pacific, northeastern Canada and West Greenland, and it too may eventually be shown to extend across the intermediate northern Canadian region. The Pacific origin of these is highly probable. Several other species, among them *Lophaster furcifer*, *Solaster endeca*, *Solaster papposus*, *Ophiopholis aculeata*, *Ophiura sarsi*, *Stegophiura nodosa*, *Strongylocentrotus droebachiensis* and *Cucumaria calcigera*, have been suggested by Mortensen (1932) as being of probable Pacific origin. Six species (25%), however, are limited to the area north of the Atlantic, and are not recorded from the Pacific. They are *Heliometa glacialis*, *Stephanasterias albula*, *Urasterias lincki*, *Gorgonocephalus arcticus*, *Ophiopus arcticus* and *Ophiocten sericeum*.

Thirteen species (54%) are predominantly arctic and subarctic in distribution: *Heliometa glacialis*, *Solaster endeca*, *Stephanasterias albula*, *Urasterias lincki*, *Leptasterias groenlandica*, *Asterias polaris*, *Gorgonocephalus arcticus*, *Amphiura sundevalli*, *Ophiopus arcticus*, *Stegophiura nodosa*, *Myriotrochus rinki*, *Cucumaria calcigera*, *Psolus fabricii*.

Ten species (42%) occur in arctic and subarctic and also extend southward into boreal waters: *Ctenodiscus crispatus*, *Pteraster militaris*, *Lophaster furcifer*, *Solaster papposus*, *Ophiacantha bidentata*, *Ophiopholis aculeata*, *Ophiura sarsi*, *Ophiura robusta*, *Ophiocten sericeum* and *Strongylocentrotus droebachiensis*.

The *Calanus* echinoderms compare most closely with the echinoderm fauna of West Greenland, from where all the species listed here have been recorded.

Only 4 species were taken in all 4 areas of the *Calanus* collection: *Leptasterias groenlandica*, *Ophiacantha bidentata*, *Ophiura sarsi* and *Strongylocentrotus droebachiensis*. Four species were restricted to Ungava Bay only: *Ctenodiscus crispatus*, *Pteraster militaris*, *Urasterias lincki* and *Cucumaria calcigera*. Two species were found only in Frobisher Bay: *Lophaster furcifer* and *Ophiopus arcticus*.

SUMMARY

1. The material includes about 1,200 specimens of echinoderms collected by the *Calanus* expeditions of 1947 to 1952 in Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound, in the eastern Canadian arctic.

2. Among the 26 species collected are one crinoid, 10 asteroids, 9 ophiurans, one echinoid and 5 holothurians, of which 6 asteroids, 5 ophiurans and 4 holothurians are new records for the collection areas.

3. One species name, *Henricia eschrichti eschrichti*, is new for arctic America; specimens of the same form, however, probably have been recorded formerly as *Henricia sanguinolenta*.

4. The distributions of 24 of the 26 species collected are well known. Of these 24 species, 14 (58%) are circumpolar or probably so, 13 (54%) are restricted largely to the arctic and subarctic areas, and 10 (42%) are found in arctic, subarctic and boreal waters. Eighteen species (75%) are recorded from the North Pacific, and all but two (*Asterias polaris* and *Cucumaria japonica*, known from the Pacific and in the Atlantic area only as far east as Greenland) are found widely in the North Atlantic region.

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Blood Levels of Hemoglobin and Lactic Acid in some Freshwater Fishes Following Exercise^{1,2,3}

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ABSTRACT

During the summers of 1953 and 1954 the effects of forced activity on two blood constituents were investigated in seven species of fresh-water fishes, representing six families. The fish were hatchery-raised or captured from lakes in the southern Okanagan Valley, and the experiments were carried out in the Summerland Trout Hatchery, Summerland, B.C. Following forced exercise for 15 minutes in water at 11.5°C. the hemoglobin level increased significantly in only one species and the lactic acid increased significantly in all species. There appears to be a correlation between the average value of lactic acid following exercise and the activity of the fish, and also with the position of the species with respect to summer water temperature.

INTRODUCTION

ONE of the primary chemical mechanisms that provide energy for muscular contraction is the anaerobic glycolysis of carbohydrate to lactic acid. The quantitative relationships between the production of lactic acid, the disappearance of glycogen and glucose were summarized for the animal kingdom by Ritchie (1928). More recent data on the subject have been compiled by Mommaerts (1950) and Dubuisson (1954).

The following resumé of the physiological chemistry of lactic acid is taken mainly from Peters and Van Slyke (1946). As a result of very vigorous muscular activity lactic acid is released in such quantities that it diffuses out of the muscles to the extracellular fluid including the circulating blood. While some of the lactic acid may be metabolized at the production site, and some utilized as the blood passes through the heart, the bulk of the lactic acid is transported to the liver where much of it is built up to glucose and finally to glycogen. Some of the glucose is carried back to the muscles to be synthesized into muscle glycogen (Cori cycle). Another important result of the lactic acid production is the immediate demands made upon the buffering systems. Indeed the lactic acid is present as lactate within the pH range compatible with life.

The importance of the lactic acid to acid-base relationships in fish blood was appreciated by von Buddenbrock (1938). He observed in marine fish that had struggled to death in a confined space that lactic acid had accumulated in the blood, and that partial hemolysis and reduction in oxygen capacity of the

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blood had also taken place. Secondat and Diaz (1942) observed in the tench that the blood lactic acid level had increased to 53 mg. per cent (53 mg. per 100 ml. of blood) in response to muscular exercise, as against 100 mg. per cent or more for man (Dill, Edwards, Newman and Margaria, 1936). Auvergnat and Secondat (1942) demonstrated that the plasma pH and CO_2 fell while the total osmotic pressure increased immediately following muscular activity in the carp. Later Secondat (1950) showed that the oxygen capacity of blood of the carp was reduced as a response to exercise.

The Bohr effect, or the influence of carbon dioxide in depressing the equilibrium between hemoglobin and oxygen, is not great in the carp (Black, 1940). Accordingly lactic acid must produce an even greater influence on the blood gases of other more CO_2 -sensitive fishes, for unlike the condition in mammals where the Bohr effect is the same, there is a very wide range in the Bohr effect in fish blood, from species to species, in both marine and fresh waters (Krogh and Leitch, 1919; Root, 1931; Willmer, 1934; Black, 1940). The present study was undertaken to determine the blood levels of lactic acid in a number of fishes that differ in CO_2 sensitivity (Black and Black, 1950) following strenuous activity, in order to relate the lactic acid levels to the Bohr effect.

The scope of the study was extended to include observations on the hemoglobin levels which provide an indication of the condition of the fish and a measure of the buffering capacity (Redfield, 1933).

In 1953, studies were made on six species from six families of freshwater fishes found in British Columbia. During 1954, the work was repeated and new data were obtained on a second member of the minnow family, and on two-year-old Kamloops trout.

MATERIALS AND METHODS

Common and scientific names and the families represented are listed in Table I, in the taxonomic order as given in Carl and Clemens (1953). All experiments were carried out at the Summerland Trout Hatchery, Summerland, British Columbia, which hatchery is operated by the British Columbia Game Department. The particular sources of the fish and the method of storing them were the same as given in detail in a previous study of upper lethal temperatures (Black, 1953). The chub used in 1954, the squawfish and largemouth bass were caught by angling; the rest were captured in a seine except the Kamloops trout which were reared in the hatchery.

All fish were held in captivity for at least a week before using. In all instances, the fish were free from obvious disturbances for at least 12 hours before the experiments were carried out.

The standard exercise interval was 15 minutes, carried out by chasing the fish continuously in a standard hatchery trough. The water temperature was 11.5°C ., or occasionally up to 12.0° , and the average oxygen level was 139 mm. Hg.

As recognized by many biologists and clearly enunciated by Barcroft (1938), the state of maximum activity is not difficult to assess. Quite the contrary holds for the resting state. Indeed, the fish may not have been in a truly

resting state during the day as shown by Spoor (1946). Because of these difficulties, and the certainty that the fish was no longer rested once capturing was begun, the term "unexercised state" is used rather than "rested state" to denote the basis of comparison with the condition where the fish had been exercised for 15 minutes.

Both control and exercised fish were captured by hand as adroitly and quickly as possible. The fish was then placed ventral side up in a V-shaped trough as illustrated in Figure 1. Care was taken to hold the fish firmly without appearing to interfere with breathing movements.

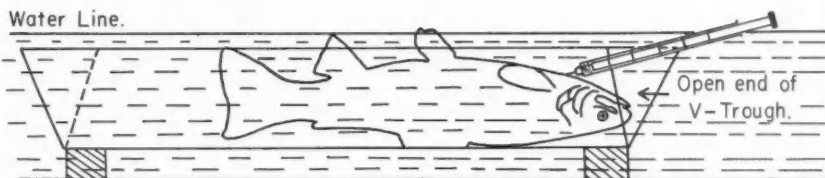


FIGURE 1. Illustration of the method used in taking a blood sample while the fish continued to respire in water.

The time taken to capture unexercised fish from the first moment of disturbing them to placing them in positions for taking blood was 30 to 60 seconds, while exercised fish were placed in 10 to 15 seconds. The time taken to draw blood from the unexercised fish was from 30 to 75 seconds. In three-fourths of the cases the blood was drawn for exercised fish in a minute or less, but in some cases up to six minutes was required. Blood was drawn from the heart.

Throughout this study, a single fish was used only once for blood sampling. That is, blood was not taken from a rested fish, which would be then exercised and used for the second sample. The experiments were planned so that most of the data for the unexercised and exercised states were paired.

The size of the sample of blood obtained was 0.3 to 0.6 ml. for fish that weighed up to 100 g. This corresponds to about 10 per cent of the total blood volume (Martin, 1950).

The blood was drawn into a hypodermic syringe that had been rinsed with paraffin oil and then 0.05 ml. of a solution of heparin was introduced and the excess rejected. One portion of the heparinized blood was immediately transferred to 0.1 normal hydrochloric acid for the photolorimetric determination of hemoglobin as acid hematin. A second sample of blood was immediately transferred to 0.66 normal sulphuric acid as a preliminary step to protein precipitation by tungstic acid. Lactic acid was determined photolorimetrically by the Barker-Summerson method. The procedures followed for each method were those given by Hawk, Oser and Summerson (1947).

As regards statistical treatment, the standard error of the average was computed for most of the data (Table I). Fisher's *t* test was applied for the significance of the difference between averages of two sets of data. Three

significant figures are given for the standard errors for the convenience of the reader who may wish to determine additional *t* tests.

RESULTS AND DISCUSSION

The results are presented in Table I.

TABLE I. Specific and common names, year, number of fish used, average weight, average hemoglobin and average lactic acid of whole blood taken from yearling and two-year-old Kamloops trout, fine-scaled sucker, carp, chub, squawfish, largemouth bass, and northern black catfish following unexercised and exercised conditions. The fish were exercised for 15 minutes in water at 11.5° C. The standard error of the average follows the average in each case. One asterisk denotes significant difference between averages at the 0.05 level; two asterisks at the .01 level.

Species	Year	No. of fish	Average weight	Average hemoglobin	Average blood lactic acid
			g.	g.	mg. %
KAMLOOPS TROUT (<i>Salmo gairdneri kamloops</i>)					
YEARLINGS					
Unexercised	1953	18	61 ± 1.8	10.2 ± 0.28	17.1 ± 1.34
Exercised	1953	15	64 ± 3.9	9.8 ± 0.32	100.2 ± 5.57**
Unexercised	1954	23	54 ± 3.2	11.5 ± 0.22	14.7 ± 0.93
Exercised	1954	20	51 ± 4.4	11.4 ± 0.23	99.5 ± 3.27**
Unexercised	1953/54	41	57 ± 2.0	11.0 ± 0.20	15.7 ± 1.09
Exercised	1953/54	35	57 ± 3.2	10.7 ± 0.23	99.8 ± 0.95**
TWO-YEAR OLDS					
Unexercised	1954	11	125 ± 17.8	10.1 ± 0.43	8.0 ± 0.95
Exercised	1954	11	134 ± 12.3	11.2 ± 0.30	82.2 ± 10.0**
FINE-SCALED SUCKER (<i>Catostomus catostomus</i>)					
Unexercised	1953	19	122 ± 49.1	10.2 ± 0.58	19.1 ± 2.57
Exercised	1953	19	117 ± 42.7	11.5 ± 0.50	54.4 ± 3.75**
Unexercised	1954	13	76 ± 6.0	8.8 ± 0.80	15.4 ± 2.36
Exercised	1954	15	65 ± 1.9	9.6 ± 0.42	56.4 ± 3.77**
Unexercised	1953/54	32	104 ± 29.0	9.4 ± 0.61	17.2 ± 1.93
Exercised	1953/54	34	94 ± 23.4	10.6 ± 0.43	55.3 ± 2.64**
CARP (<i>Cyprinus carpio</i>)					
Unexercised	1953	16	605 ± 67.1	11.2 ± 0.71	8.5 ± 2.69
Exercised	1953	13	595 ± 70.6	11.3 ± 0.69	54.3 ± 4.49**
Unexercised	1954	7	511 ± 61.3	10.1 ± 0.74	8.5 ± 2.98
Exercised	1954	9	572 ± 112	10.4 ± 0.73	77.6 ± 4.33**
SQUAWFISH (<i>Ptychocheilus oregonense</i>)					
Unexercised	1954	12	57 ± 6.6	9.8 ± 0.68	19.3 ± 3.99
Exercised	1954	13	63 ± 7.6	11.6 ± 0.73	94.2 ± 7.71**
LARGEMOUTH BASS (<i>Micropterus salmoides</i>)					
Unexercised	1953	6	66 ± 4.0	8.4 ± 0.67	16.9 ± 6.06
Exercised	1953	6	69 ± 3.6	10.1 ± 0.78	65.2 ± 7.78**
Unexercised	1954	7	140 ± 57.5	7.8 ± 0.60	17.0 ± 4.53
Exercised	1954	7	281 ± 124	9.7 ± 0.43	85.6 ± 3.76**
Unexercised	1953/54	13	115 ± 30.5	8.1 ± 0.43	16.9 ± 3.51
Exercised	1953/54	13	183 ± 71.7	9.9 ± 0.42*	76.2 ± 4.90**
NORTHERN BLACK CATFISH (<i>Ameiurus melas melas</i>)					
Unexercised	1953	10	131 ± 16.7	11.3 ± 0.53	9.0 ± 2.27
Exercised	1953	11	153 ± 19.5	11.2 ± 0.56	33.1 ± 3.68*
Unexercised	1954	2	136	10.1	6.4
Exercised	1954	8	74 ± 12.5	11.2 ± 0.66	37.4 ± 11.70
Unexercised	1953/54	12	132 ± 13.9	11.1 ± 0.47	8.6 ± 1.91
Exercised	1953/54	19	120 ± 15.3	11.2 ± 0.41	34.9 ± 2.64**

BEHAVIOUR DURING ONSET OF FATIGUE

The pattern of fatigue in the yearling Kamloops trout appeared to be uniform for each experiment. During the first minute the fish darted away from the source of stimulation at a speed of approximately 16 kilometers per hour (10 m.p.h.). Within 5 minutes and often within 3 minutes, the maximum swimming speed was reduced to approximately 3.2 kilometers per hour (2 m.p.h.). Most of the fish would stop swimming and rest on the bottom of the trough at the end of 3 minutes, if permitted. During some recovery experiments, to be reported later, 3-5 fish were exercised at a time. In these experiments the fish invariably swam together as a school, and as invariably stopped schooling between the 3rd and 5th minute of exercise. Moreover, the escape pattern of the fish changed within this time interval of 3-5 minutes, for the fish appeared to look for protection in the darker corners of the trough rather than escape by swimming. During 1953 some of the Kamloops trout appeared to be refractory to stimulation before the end of 15 minutes. This was not the case in 1954. In a few cases the fish were allowed to rest for 3-5 minutes after 5 minutes of exercise. These fish were then capable of a sustained spurt of rapid swimming for 10-15 seconds. No blood samples were taken from these fish.

The pattern of fatigue for the chub and squawfish was very similar to that seen in the Kamloops trout yearlings. However, the squawfish exhibited one facet of behaviour not seen in the other species: during the first few minutes of forced exercise they often broke through to nearly clear the surface of the water. The remaining species also showed relatively rapid bursts of swimming activity at the outset, and then slowed down and sought cover after 3-5 minutes. Estimates were made on swimming rates only in the Kamloops trout yearlings.

HEMOGLOBIN

UNEXERCISED STATE

Hemoglobin values for the unexercised fish are of the same order as values reported elsewhere. The average value of 11 grams per cent for yearling and 10.1 grams per cent for the two-year-old Kamloops trout are near the value of 10.3 grams per cent reported by Irving, Black and Safford (1941), for the rainbow trout, a related sub-species. The value of 9.4 grams per cent of the fine-scaled sucker is higher than the value reported by Black (1940) of 7.9 grams per cent for the common sucker (*C. commersoni*). The average of 10.9 grams per cent for the carp is compared with 9.4 grams per cent reported by Black (1940). However the value of 8.1 grams per cent for the largemouth bass is less than the 10.3 grams per cent reported for the same species by Hiestand (1951). The value of 11.1 grams per cent for the northern black catfish is compared with a value of 9.9 grams per cent for the brown catfish (*A. nebulosus*) reported by Black (1940).

EXERCISED STATE

The effect of exercise upon the average hemoglobin value was variable, and in only one case, that of the 1954 largemouth bass, was there a significant in-

crease in hemoglobin following exercise. This increase may reflect an osmotic shift of water from the blood in the tissues in response to metabolic activity accompanying muscular activity. Recruitment of red cells from hemopoietic tissues cannot be excluded as another source of increased hemoglobin content. The increase in average hemoglobin following activity in no way excludes the possibility that the oxygen capacity may have been reduced by fatigue products as Secondat (1950) found for the carp.

LACTIC ACID

UNEXERCISED CONDITION

Average values for the unexercised condition are in two ranges, i.e. 8-9 mg. per cent for two-year-old Kamloops trout, chub, carp and northern black catfish; and 16-19 mg. per cent for the yearling Kamloops trout, fine-scaled sucker, squawfish and largemouth bass (Table I). All the values are probably higher than those for the completely rested condition. The values for man at complete rest range from 8 to 16 mg. per cent (Peters and Van Slyke, 1946), and 28.5 ± 4.4 mg. per cent in rested but not basal condition (Crescitelli and Taylor, 1944).

EXERCISED CONDITION

In all cases there was a significant increase in the average blood lactic acid level after strenuous activity (Table I). These findings are in harmony with the findings of Secondat and Diaz (1942) for the tench, and with the condition in mammals (Peters and Van Slyke, 1946). If there is a consistent relation between blood lactic acid and the lactic acid concentration at the production site in the muscles, as there probably is, then the increase in lactic acid in fishes following muscular activity is in keeping with the whole comparative series, including certain invertebrates (Ritchie, 1928).

A comparison of the results obtained in 1954 with those of 1953 provides a measure of the reproducibility of the data. The average values for the exercised condition for Kamloops trout yearlings, fine-scaled sucker and northern black catfish were consistent for the two years, whereas those for the carp and chub were significantly higher in 1954. The agreement in the data for the Kamloops trout yearlings for the two years affords considerable confidence in the methods. Undoubtedly the fish were subjected to the same conditions of temperature and oxygen pressure, and were given the same care in feeding and rearing by the hatchery staff. The higher 1954 values in the chub compared with 1953 may be associated with the fact that in 1954 the fish were angled whereas in 1953 they were seined. No explanation is offered for the difference in values in the carp for the two years. However, residual effect of temperature may have contributed to the differences both in the chub and carp.

When the fish are placed in the increasing magnitude of the average values for lactic acid following exercise, including the data of Secondat and Diaz (1942) for the tench, the following order is obtained: northern black catfish, tench, fine-scaled sucker, carp, largemouth bass, squawfish, chub and yearling

Kamloops trout. The particular order for the last three named depends on the criteria selected (averages for the two years, and age of the Kamloops trout). Except for the Kamloops trout and the chub, the order for the two years for the respective species is the same.

The primary purpose of this study was to determine the blood levels of lactic acid following activity in view of the wide range of the Bohr effect in fish blood. As noted earlier, Secondat (1950) showed that there was a marked reduction in oxygen capacity of carp blood following activity, yet the Bohr effect in the carp is not great compared with that in the common sucker and trout (Table II, column 7). It will be noted from columns 7 and 8 of Table II that the Bohr effect increases in the same order as the lactic acid concentration. Yet to accommodate the Bohr effect, the lactic acid should be low for the trout and could be high for the catfish, so far as acid is concerned. As regards the very sensitive blood of the common sucker, Black and Irving (1938) showed that a concentration between 150 and 400 mg. per cent of lactic acid caused hemolysis *in vitro*. It would appear that the press of acid metabolites on respiration and even on survival must be very great in many active species.

Black, Fry and Black (1954) have shown that there are considerable specific differences in the utilization of oxygen in abnormally high concentrations of carbon dioxide in the respiring medium. They contended that much of the

TABLE II. Probable acclimation temperatures, upper lethal temperatures, limiting oxygen tension, influence of carbon dioxide on oxygen utilization, oxygen affinity of hemoglobin, Bohr effect on hemoglobin and blood levels of lactic acid following vigorous activity in a number of freshwater fishes. The data are listed in the increasing order of lactic acid values. Sources: (a) Black, 1940; (b) Brett, 1944; (c) Black, Fry and Black, 1954; (d) Black, 1953; (e) Black and Black, 1950; (f) Hart, 1947; (g) Fry, Hart and Walker, 1946; (h) Black, 1955; (i) this paper.

1 Species	2 Probable accli- mation temp.	3 Upper lethal temp.	4 Limiting oxygen tension at death from hypoxia	5 Carbon dioxide effect upon oxygen use at pO ₂ 160 mm. Hg	6 Oxygen affinity of hemoglobin pO ₂ mm. Hg at 50% HbO ₂ , 15°	7 Bohr effect as increase in pO ₂ on increasing pCO ₂ 10 mm. Hg	8 Blood lactic acid after 15 minutes' activity at 11.5°
	° C.	° C.	mm. Hg	mm. Hg	mm. Hg	mm. Hg	mg. %
Brown catfish (<i>Ameiurus nebulosus</i>)	5-15	1.4 (a)	4.3 (a)	...
	19-22	33.3 (b)	4 (c)	338 (c)
Northern black catfish	23	35.0 (d)	3 (e)	386 (e)	35 (i)
Carp	5-15	5 (a)	6.7 (a)	...
	26	35.7 (d)	4 (e)	186-260 (e)	54-78 (i)
Fine-scaled sucker	14	26.9 (d)	6 (e)	172-186 (e)	55 (i)
Common sucker (<i>Catostomus commersoni</i>)	5-15	12 (a)	33 (a)	...
	20	30.0 (f)	9 (c)	107 (c)
Largemouth bass	20-21	28.9 (d)	4 (e)	125 (e)	76 (i)
Squawfish	19-22	29.3 (h)	6 (h)	170 (h)	94 (i)
Chub (<i>Mylocheilus caurinum</i>)	10-14	27 (d)	8 (e)	205-284 (e)	82-116 (i)
Kamloops trout	11.5	24.0 (d)	14 (e)	110-114 (e)	100 (i)
Brook trout (<i>Salvelinus fontinalis</i>)	11.0	24.0 (g)
	20	...	19 (c)	132 (c)	13 (h)	36 (h)	...

effect of carbon dioxide must operate through the Bohr effect. From the data presented here on lactic acid (Table II, column 8) in relation to lethal concentrations of carbon dioxide (column 7), it is clear that some of the influence attributed to the Bohr effect may be due to lactic acid. If the Bohr effect in the northern black catfish is the same as in the brown catfish, then the great resistance to external carbon dioxide may be due not only to a low Bohr effect but possibly to less lactic acid elaborated during hypoxia. In the same manner it may be argued that part of the sensitivity to external carbon dioxide in the trout may be due to greater release of lactic acid as hypoxia occurs. This hypothesis remains to be tested.

Many specific differences in physiological and biochemical characteristics have been demonstrated in fish. These studies include: Wells' work on resistance of freshwater fishes to carbon dioxide and oxygen (1913) and carbon dioxide and monoxide (1918); Huntsman's (1926) study for marine fish and Hathaway's (1927) work on freshwater fish on upper lethal temperatures; the study of Wiebe *et al.* (1934) on difference in ability of fish to utilize oxygen at different pH levels; Powers' (1932) demonstration of the effect of carbon dioxide upon oxygen utilization and the observation by Fry and Black (1938) that this effect of carbon dioxide is correlated in part with the temperature habitat of the fish; Black's (1940) observations that both the oxygen affinity of the hemoglobin and the Bohr effect differed and that these differences may be related also to the temperature habitat; the extension of Wells' study by Black, Fry and Black (1954) in that the limiting oxygen tension at death seemed to be related to temperature habitat. Certain of these and other influences on the activity of fishes have been analysed and rationalized by Fry (1947) in his publication on the relation of environmental factors to animal activity.

The data presented here on blood levels of lactic acid following activity reveal another scale of differences which may be related to temperature habitat and also to activity. Yet, as discussed above, there is an antithesis presented by the graded Bohr effect and the graded series of blood levels of lactic acid. The following hypothesis is presented as an explanation for the various differences in freshwater fishes. It is suggested that the underlying structure for all the species biochemical and physiological differences is the expression of a biochemical constitution to meet the most decisive of factors, namely, environmental temperature, particularly the temperatures of mid-winter and late summer.

At the warm-water end of the scale is the catfish, the blood of which is suited to the transport of oxygen at higher temperatures, and which blood is well suited to acid, that is a low Bohr effect. The catfish survives a low oxygen tension and hence the fish is better fitted to meet the two arms of a pincers imposed by increased environmental temperature, namely, a decreased solubility of oxygen in the external breathing medium at the very time when the tissue demand for oxygen is driven upward by a higher body temperature. The supposition is made that the low level of lactic acid in the blood following maximal activity at 11.5°C. would be increased at higher temperatures, but that the increase would not be so great as to cause lethal acidosis in the catfish. The

northern black catfish has the highest lethal temperature when acclimation temperature is considered (Table II, columns 2 and 3). Paul and Fry (see Fry, 1947) made the interesting discovery that the scope for activity in the brown catfish continues to increase with temperature practically to the upper lethal point. This accomplishment on the part of the catfish is interpreted as the effect of upward drive of metabolism and a failure to develop acidosis from such metabolites as carbonic and lactic acid sufficient to influence the lethal temperature, that is, a failure to summate lethal effects of acidosis with the lethal effects of temperature.

The trout is adapted to colder water. The oxygen affinity of the hemoglobin is low, and the Bohr effect is moderately great; both features are adaptations to lower temperatures. The limiting oxygen tension is high. The blood level of lactic acid following vigorous muscular activity at 11.5°C. is relatively high, being of the same order as in man. The relatively low upper lethal temperature limits survival to lower temperatures than in the catfish or carp. Job (1955) working in Fry's laboratory has shown that the scope for activity in the brook trout falls off sharply as the temperature is increased, mainly owing to a steep rise in resting metabolism. The decline in scope appears well below the upper lethal temperature. This decline in scope for activity is interpreted as being primarily due to the incipient lethal effect of temperature *per se* combined with the progressive debilitating effect of acidosis resulting from muscular activity, and from the increased metabolic load arising from temperature itself. Moreover, both the circulatory and respiratory systems will be increasingly taxed, for the solubility of oxygen in the external medium will be reduced at the higher temperature.

It is interesting to speculate on the possible relation of the characteristics of suckers listed in Table II with reference to their distribution. The hemoglobin of the common sucker possesses a moderately low affinity for oxygen, and a very great Bohr effect. These are features which confer an advantage to the sucker for activity at lower temperature. At the same time the blood level of lactic acid in the fine-scaled sucker at 11.5°C. was not very great compared with that in the Kamloops trout. The upper lethal temperatures for the common sucker acclimated to 20° was 30°C., and for the fine-scaled sucker 26.9° for acclimation at 14.0°C. Thus the suckers are better adapted for activity at lower temperature than the carp, and better adapted to survive warmer waters than the trout. In British Columbia, at least, the suckers have a very wide distribution geographically (Carl and Clemens, 1953).

As Fry (1947) has demonstrated, it is essential to distinguish between the factors that make for tolerance toward and survival of a given temperature, and the capacity for activity. In the previous discussion, lactic acid production has been related to temperature and the level of metabolism. Lactic acid may also be related to activity. At present, however, it seems unwise to press the relationship too far, for the fundamental correlate with activity is probably more closely related to the quantity of muscle glycogen and lactic acid in the muscle than the derived blood level of lactic acid. The quantity of myoglobin present as one

determinant of the metabolic pathway for oxygen should also be known. With these reservations, the observations by Fry and his associates on the scope for activity at 10°C. are presented in Table III for comparison. While allowance must be made for difference in species, there is some relation between the scope for activity for the brown catfish and the rainbow and brook trout and the blood level of lactic acid following activity in the related northern black catfish and Kamloops trout, respectively.

TABLE III. The scope for activity at 10° C. for some freshwater fishes. The scope is expressed as the difference between maximal and minimal utilization of oxygen in ml. of oxygen per kg. per hour.

Species	Weight	Oxygen	Authority
	g.	ml./kg./hour	
Brown catfish	10	84	Paul and Fry (see Fry, 1947)
Rainbow trout	30	175	Graham and Gibson, 1948
Brook trout	5	190	Job, 1955
	15	167	Job, 1955

There are objections to the hypothesis, including the following: data are not complete for any one given species; acclimation to temperature is not always known or controlled; acclimation to oxygen level is not always known, and this factor has recently been shown by Shepard (1955) to be important in the brook trout; the distribution of the species in a given body of water is not well known, the important factors of size, weight and sexual maturity, reproductive stage and endocrine state have not been determined for all the features listed; too little is known about the activity of fishes; very little is known about the quantities of glycogen and lactic acid in the muscles in fishes; data on the several biochemical and physiological characteristics for the lower, mid and upper positions of the viable temperature tolerance remain to be obtained.

Despite the many variables and the wide gaps in knowledge just enumerated, there appears to be a correlation between a number of physiological and biochemical adaptations to temperature, metabolism and the distribution, activity and survival of freshwater fishes.

SUMMARY

1. The hemoglobin level following forced exercise for 15 minutes increased significantly over the unexercised level in only one species, the largemouth bass. This change is attributed to an osmotic shift of water from blood to muscle.

2. The average blood levels of lactic acid for the unexercised state are in two ranges, i.e. 8-9 mg. per cent for the two-year-old Kamloops trout, chub, carp and northern black catfish; and 16-19 mg. per cent for the yearling Kamloops trout, fine-scaled sucker, squawfish and largemouth bass.

3. There was a significant increase in the blood level of lactic acid following exercise in all seven species examined. The quantitative levels differed, however; the averages expressed as mg. per cent were as follows: northern black catfish,

34.9 ± 2.6 ; fine-scaled sucker, 55.3 ± 2.6 ; carp, 54.3 ± 4.5 in 1953, and 77.6 ± 4.3 in 1954; largemouth bass, 76.2 ± 4.9 ; squawfish, 94.2 ± 7.7 ; chub, 81.6 ± 9.0 in 1953, 116.0 ± 9.0 in 1954; Kamloops trout yearlings, 99.8 ± 0.9 ; Kamloops trout two-year-olds, 82.2 ± 10.0 .

4. There is an indication that the lactic acid produced in the northern black catfish and Kamloops trout at 11°C . is related to their capacity for activity at that temperature.

5. The order for the blood levels of lactic acid is correlated with upper lethal temperatures except in the fine-scaled sucker and chub. The catfish and carp have high upper lethal temperature, the trout has a low one. There are other physiological and biochemical characteristics, such as oxygen affinity of the blood, Bohr effect, limiting oxygen tension, effect of carbon dioxide on oxygen utilization, which show species differences. All these features show some relation to the capacity of the species to tolerate temperature and activity at a given temperature. There is also an obvious relationship of these characteristics in the different fishes to the position taken with respect to temperature in nature. A hypothesis based on metabolic level and specific characteristics adapted to cold or warm temperature is presented to account for the specific biochemical and physiological differences observed.

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Age, Maturity, Spawning and Food of Burbot, *Lota lota*, in Lake Winnipeg¹

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ABSTRACT

Burbot are common in Lake Winnipeg; 886 were taken as a sample. Trap-net and otter-trawl catches are more representative of the population than gill-net catches. A significant difference in length-weight relationship exists between two localities. Ages were determined from otoliths. Heavier exploitation in the northern part of the lake probably accelerated the growth rate. Age-6 burbot there weighed 3.4 pounds compared with 2.6 pounds in the southern part. Spawning begins about January 31 and lasts 3 weeks. The smaller burbot feed mainly on insect larvae, the larger burbot on fish and crayfish.

INTRODUCTION

PERSONNEL of the Central Fisheries Research Station have studied the summer commercial fishery in the northern part of Lake Winnipeg since 1948. The study was concerned mainly with the lake whitefish, *Coregonus clupeaformis*, but data for other species, including the burbot, were recorded. The fraction of the fishery under special study amounted to about 15 per cent of the whole. From this fraction of the fishery, summer catches of all species of fish combined totalled 300,000 to 900,000 pounds annually. Burbot, which usually ranked second by weight in the catches, amounted to about 20 per cent of the total weight of fish which were studied.

At the close of the summer fishery attention was directed to the fall and winter fisheries in the southern part of the lake. In these fisheries as well, the burbot occupies a prominent position.

In some parts of the United States burbot are considered a game fish (Bjorn, 1940), but in Canada, where it occurs in most lakes, it is regarded as a nuisance by commercial fishermen. In Lake Winnipeg, burbot are found in such quantities that they adversely affect the gill-net fishery. Much time is wasted in removing them from the nets, and some potentially productive grounds are avoided because of their presence. Burbot are seldom marketed, and only for use as domestic mink food where its low price is increasing its popularity.

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METHODS

Burbot were sampled with three types of fishing gear; trap-nets, otter-trawl and gill-nets.

The trap-nets were Lake Erie type, large structures of netting, completely submerged, and held in a certain shape in the water by the combined action of floats, weights and anchors. The interior of the large enclosure is fitted with baffles which make it difficult for a fish to find its way out, but easy to enter.

The otter-trawl used was the type known on the Atlantic coast as a flounder drag. This type of gear is dragged along the bottom to engulf the fish in its path. The otter-trawl and the trap-nets were operated experimentally by the investigators.

Also fished experimentally was a series of gill-nets ranging in mesh size from 1½ inches to 5¼ inches stretched measure (38–133 mm.) from which burbot were sampled. Burbot were sampled also from commercial fishermen's gill-net catches.

The numbers of burbot sampled by these various means are shown in Table I. Most were taken in trap-net catches off Mukutawa River during June and July of 1950, 1951 and 1953, and many by the same method off Winnipeg Beach during October, 1954 (Fig. 1). Samples were taken from gill-net catches near Hecla Island, Catfish Creek, and Black Bear Island from August through October, 1950, and from Kinwow Bay during February, 1952. A few were taken from otter-trawl catches at Bull Head in November, 1953.

Burbot were weighed individually to the nearest tenth of a pound, and stomachs were examined immediately. Sex and maturity were determined by an examination of the gonads. Total length, in inches, was recorded only for burbot sampled in 1951 at Mukutawa River, and at Winnipeg Beach in 1954.

TABLE I. Numbers of burbot sampled by means of various gear from Lake Winnipeg.

	Gill-nets, mesh 1½ to 5¼ inches	Gill-nets, mesh 3¼ inches	Otter-trawl	Trap-net	Total
Hecla					
1950	33	33
Catfish Creek					
Blackbear I.					
1950	...	61	61
Kinwow Bay					
1952	...	43	43
Bull Head					
1953	30	...	30
Winnipeg Beach					
1954	303	303
Mukutawa River					
1950	236	236
1951	133	133
1953	47	47
Total	33	104	30	719	886

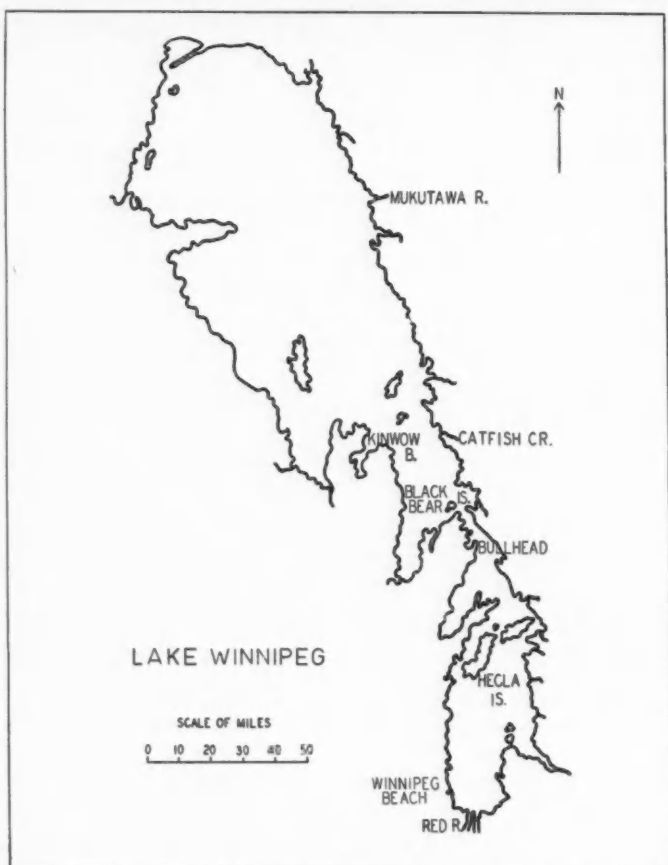


FIGURE 1. A map of Lake Winnipeg showing sampling localities.

To remove otoliths for age determination, a median incision was made in the skull with a heavy, pointed knife. When properly executed one stroke bisects the brain without displacing the parts. The burbot then was turned on its side with dorsal surface nearest the operator, and two downward transverse cuts were made, about an inch apart, extending distally from the original cut. The three-sided section thus formed, hinged on the fourth side, was pried open to expose the brain, and the two otoliths which lie on either side of the mid-brain were easily removed with forceps.

The otoliths were stored in small envelopes. Later, many were transferred to a water solution of glycerine when it became evident that they were deteriorating. This method of preserving was found to be relatively ineffective; Clemens (1951) reports a more satisfactory way. After this experience, otoliths

were examined as soon as possible before they became excessively opaque, because these are difficult to read.

When otoliths were too opaque, the convex or both surfaces were smoothed with a file or small emery wheel to allow the light to penetrate. In a few cases, otoliths had deteriorated to such an extent that age determinations were impossible, and data for these specimens were discarded.

To determine age, otoliths were immersed in water in a watch glass, and examined with a low power microscope. The method used has been described by Clemens (1951) and the interpretation of the dark and light rings is based on that of Martin (1941). Dark, or winter rings were considered as birthdays and the ages are therefore recorded in completed years. That is, a fish recorded as age 3 is in its fourth year.

LENGTH-WEIGHT RELATIONSHIP

Both length and weight were recorded for 133 specimens at Mukutawa River and for 303 specimens at Winnipeg Beach. Both samples were from trap-nets although taken during different years. Average lengths and weights at each age are shown in Table II.

TABLE II. The average length and average weight of burbot of known ages at two localities on Lake Winnipeg. Sexes are combined.

Age	Winnipeg Beach			Mukutawa River		
	Average length	Average weight	No. of fish	Average length	Average weight	No. of fish
	<i>in.</i>	<i>lb.</i>		<i>in.</i>	<i>lb.</i>	
3	16.2	1.3	4	14.7	0.7	5
4	19.3	2.2	16	18.1	1.8	29
5	20.7	2.4	16	20.1	2.5	30
6	20.9	2.6	29	22.3	3.4	42
7	21.8	2.9	54	24.2	4.6	15
8	23.1	3.7	50	26.6	6.0	6
9	24.9	4.9	57	28.3	8.6	1
10	26.3	4.9	20	28.3	8.4	4
11	28.4	6.6	22
12	30.8	7.8	18	32.3	10.2	1
13	31.3	8.4	11
14	31.0	7.4	6
Total	24.1	4.3	303	21.3	3.3	133

When the logarithm of the average length is plotted against the logarithm of the average weight at the various ages, the resulting curves for males and females approximate each other closely for each locality. Sexes were therefore combined in order to compare localities.

Since the points representing the logarithms of average length and of average weight at the various ages tend to lie along a straight line, it is possible to use a standard method of co-variance described by Snedecor (1946) to compare the two samples. An outline of the method is presented in Tables III and IV.

TABLE III. Some statistics for analysis of covariance of length-weight relationship of 2 populations of Lake Winnipeg burbot.

	Mukutawa R.	Winnipeg Beach	Combined populations	Average within populations	Degrees of freedom	Sum
n	9	12	21
SX	12.298	16.577	28.875
SY	5.337	7.165	12.502
SX ²	16.899136	22.992125	39.891261
SXY	7.620926	10.156720	17.777646
SY ²	4.318481	5.010215	9.328696
Sx ²	0.094602	8	...
	...	0.092381	11	...
	0.186983	19	...
Sxy	0.328212	8	...
	...	0.258870	11	...
	0.587082	19	...
Sy ²	1.153640	8	...
	...	0.732113	11	...
	1.885753	19	...
Sums of squares of errors of estimate	0.014942	7	...
	...	0.006728	10	...
	0.042456	18	...
	17	0.021670

TABLE IV. Analysis of covariance of length-weight relationship of 2 populations of Lake Winnipeg burbot.

Source of variation	Degrees of freedom	Sums of squares	Mean square	F
Total	19	0.051878
Average within populations	18	0.042456	0.0023586	...
Between mean lengths	1	0.009422	0.009422	3.995
Deviation from individual change rates	17	0.021670	0.0012747	...
Between change rates	1	0.020786	0.020786	16.306**

For the difference between mean lengths at a comparable weight, $F = 3.995$ with 1 and 18 degrees of freedom; and for the difference between rates of change of length with changing weight, $F = 16.306$ with 1 and 17 degrees of freedom. These values indicate that the difference in mean length at a comparable weight is not significant, whereas the differences between the rates of change are highly significant. For all burbot that weigh over 4 pounds, Mukutawa River fish are shorter per unit weight than Winnipeg Beach fish, while the opposite is true of fish that weigh less than 4 pounds.

Routine studies of the commercial fishery showed that the commercial gill-nets at Mukutawa River selected mainly larger fish whereas the gill-nets at Winnipeg Beach, which are of a much smaller mesh size, exploited the smaller fish. The smaller mesh nets probably do not exploit the burbot efficiently; thus the Winnipeg Beach burbot may be virtually an unexploited population. This might account for the difference in the length-weight relationship.

The length-weight relationship for the Mukutawa River sample may be expressed by the equation

$$y = 0.00017x^{3.18}$$

where y = weight in pounds
and x = total length in inches

The equation for similar data for Winnipeg Beach is

$$y = 0.00085x^{2.65}$$

Both equations are based on lines fitted by inspection to points which represent average length and weight at a given age with little weight given to points which represent averages that are based on few fish.

GROWTH CURVES

The relationship between average weight and age among burbot is shown in Table II. These fish were taken from trap-net catches made at two localities and the sexes are combined. Burbot smaller than 3 pounds are probably not fully represented in the samples. It is presumed that the trap-net reaches full efficiency for catching this species when individuals weigh 3 pounds or more. Consequently, only fish older than 6 or 7, depending on the locality, appear to have been completely vulnerable. In spite of this, a wide range of sizes is represented.

Similar data for burbot from gill-net catches are shown in Table V. This type of gear is very selective of fish between 1.2 and 2.0 pounds. Age-weight data are shown in the lower part of the table for trawl-caught fish. The reliability of this sampling method is indicated by a good range of sizes but data are too scant to warrant further treatment.

TABLE V. The average weight in pounds of burbot from catches from gill-nets and otter-trawl. Numbers of fish are shown in parentheses.

Age in completed years										
2	3	4	5	6	7	8	9	10	11	Total
FROM GILL-NETS OF VARIOUS MESH SIZES										
0.8 (1)	1.0 (9)	1.5 (18)	1.7 (38)	1.7 (29)	1.6 (25)	1.9 (14)	2.1 (1)	3.5 (2)
									...	(137)
FROM OTTER-TRAWL										
0.2 (2)	0.8 (7)	1.1 (9)	1.4 (8)	3.5 (3)	8.2 (1)	...
										(30)

Growth curves for three groups of burbot are shown in Figure 2. In the Winnipeg Beach sample (Fig. 2A), the average weights shown for ages 4 and 5 appear to be too high. There are two possible reasons; the fish were sampled over a fairly short period and there is reason to suspect that the sample is atypical with respect to size distribution; and there may be net selection for fish which weigh less than about 2.5 pounds.

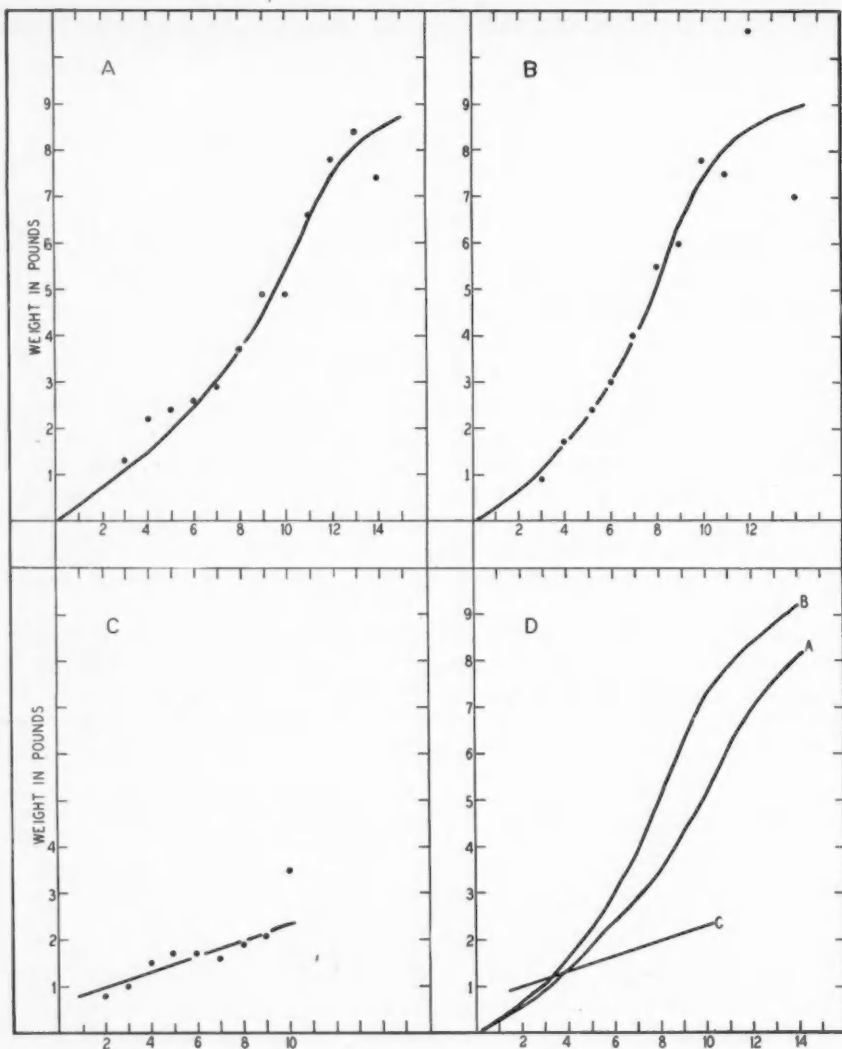


FIGURE 2. Growth curves for 3 samples of Lake Winnipeg burbot: A. Winnipeg Beach trap-net sample; B. Big Black River trap-net sample; C. gill-net sample, various localities; D. growth curves are shown together.

The growth curve for the Mukutawa River sample (Fig. 2B), fits the observed values well. The sample was accumulated over a long period (Table I), which may have improved its accuracy.

A growth curve for burbot sampled from gill-nets is shown in Fig. 2C. The sample is probably biased by net selection and affords a poor growth curve.

Mukutawa River fish grow faster than those from Winnipeg Beach (Fig. 2D). One might expect the faster growth rate to occur in the warmer southern waters, whereas the opposite is true. Studies of the commercial fisheries in each of the two areas show that the 5½-inch mesh gill-nets used near Mukutawa River exploit the burbot more effectively than the 3-inch mesh nets used in the Winnipeg Beach fishery. Since the larger mesh takes a larger average size of fish, competition is lessened among the older fish, which could account for the faster growth rate.

SEXUAL MATURITY AND SPAWNING PERIOD

Fish that on the basis of experience were assessed as having spawned at least once or to be about to spawn at the next spawning season were classed as sexually mature. Decisions were based on the relative size, shape and appearance of the gonads. The mature male gonad is angular and flesh-coloured. Gonads of immature males are similar but reduced in size. Mature female gonads are rounded, broader for their length, folds are apparent, and they are frequently discoloured by bluish blotches. Immature female gonads display the characteristic roundness of shape but are much smaller and are of uniform colour.

Immature fish were found in small numbers in all three samples, but appeared most numerous in the trap-net sample from Mukutawa River. In general, immaturity was more closely associated with weight than with age. The largest immature female weighed 1.5 pounds, and the largest immature male weighed 2.2 pounds.

The Winnipeg Beach and gill-net samples were taken later in the year than the Mukutawa River sample, that is, closer to the onset of the spawning season. Development of the gonads of mature fish was more apparent, hence the possibility that some of the Mukutawa River fish classed as immature may have, in fact, been mature. On the other hand, the colder waters from which the latter sample was taken may have been a factor in delaying sexual maturity.

At Mukutawa River some burbot probably mature by age 2 and at less than 1 pound in weight (Table VI). Immature females averaged 1.2 pounds and immature males 1.9 pounds, which suggests that females reach maturity at a lesser weight than males, possibly when younger.

Incidental observations were made on breeding fish during the study of the winter commercial fishery which encompasses the area within 120 miles of the south end of the lake. Spawning burbot were common throughout. Although the remainder of the lake was not visited in winter, it is believed that spawning occurs there as well.

Observations relative to spawning activity were recorded during each of four winters beginning in 1950. Male burbot were observed in a near-ripe condition about January 20 in each year, and actual spawning probably commenced about January 31. Many fish were spent by February 10, but ripe unspawned

fish of both sexes occurred as late as February 20. Each year an estimated 5 per cent of the mature fish on the spawning grounds appeared unripe, and unready to spawn that season.

The effects, if any, of limnological conditions on the spawning of the burbot are not known. In Lake Winnipeg spawning coincided, more or less, with the beginning of the period of minimum water temperatures. Readings varied slightly from year to year, but were approximately 1°C. at the bottom and 0°C. at the under surface of the ice at spawning time. Dissolved oxygen remained fairly constant during January and February at about 8 and 10 cc./litre for bottom and surface samples, and dissolved CO₂ varied from 10 to 13 p.p.m.

Actual spawning activity could not be observed in Lake Winnipeg because of the ice cover. However, nets which were fished at the under surface of the ice appeared to take more burbot than those fished at or near the bottom, which suggests that the spawning act was accomplished near the surface. This observation is in agreement with Cahn (1936) who witnessed spawning behaviour of burbot in a Minnesota lake. In Lake Winnipeg fish in spawning condition occurred both inshore and offshore but they were observed in greater numbers in the inshore nets.

TABLE VI. Percentage of immature burbot from Mukutawa River sampled during 1950, 1951 and 1953.

Age	Males			Females		
	No. immature	No in sample	Percentage immature	No. immature	No. in sample	Percentage immature
3	1	7	14	3	6	50
4	7	16	44	3	35	9
5	5	40	12	4	65	6
6	8	50	16	1	84	1
Total	21	113	19	11	190	6

FOOD HABITS

The stomachs of more than 500 burbot were examined at various times and places during the four years, and their contents were recorded. The stomachs from fish caught in gill-nets were frequently empty, or the contents were in an advanced state of digestion. Observations were more rewarding for stomachs from fish taken by trap-net and otter-trawl, particularly those from the latter. Unfortunately, the trawl was operated for too short a period to add much bulk to the data.

Of those examined, more than 400 stomachs were from burbot taken in trap-net catches at Mukutawa River. About 69 per cent contained food. In about one-third of stomachs in which food was present, fish was the sole item. About one-third of stomachs contained crayfish solely, while the remainder contained both fish and crayfish in varying amounts.

It was evident that many burbot captured in the trap-net took advantage of the large numbers of other fish, likewise imprisoned in the enclosure, in order

to gorge themselves. Of the several species of fish available to the burbot in the enclosure, they seemed to prefer cisco, *Leucichthys* spp. To some extent, this habit of feeding while in captivity invalidates calculations of the relative natural consumption of fish and other prey.

In a further analysis, cisco was found to be the main fish item in 34 per cent of the stomachs which contained fish. Sauger, *Stizostedion canadense*, yellow walleye, *S. vitreum vitreum* and yellow perch, *Perca flavescens* combined, were found in 7 per cent of stomachs. In 2 per cent of the stomachs, fish identifiable only as coregonines were found, while in 57 per cent of stomachs, the fish present were digested beyond recognition.

A field check on the stomachs of 30 burbot caught in the otter-trawl was made. Food was present in all but three of the stomachs, and an analysis of the stomach contents is presented in Table VII. The trawl captured a fairly wide range of sizes (Table III) and the stomach contents were, of course, very "fresh". In some instances crayfish liberated from burbot stomachs were able to crawl away. This fact would permit the fixing of the time they were ingested with reasonable accuracy. For these reasons, it appears that the trawl would be the gear most suitable with which to make a food study.

The younger burbot depended a good deal upon smaller bottom organisms for food, whereas fish and crayfish were taken mainly by older burbot. Of the 27 stomachs, 16 contained fish. Most of the fish which appeared in the stomachs were less than 5 inches in length, and were predominantly trout perch, *Percopsis omiscomaycus* and cisco. Other species which appeared, in order of abundance, were as follows: freshwater drum, *Aplodinotus grunniens*; sauger; yellow walleye; sculpin, *Cottus* spp.; darters, *Etheostomidae*; and sticklebacks, *Gasterosteidae*. Only one species of crayfish, *Orconectes virilis* (Hagen), was recognized.

TABLE VII. The occurrence of various food items noted in the stomachs of 27 burbot of various sizes taken by otter-trawl.

Item	No. of stomachs in which noted	Average size of burbot	Average age
		lb.	
Insect larvae, mostly <i>Ephemera</i> idae	9	0.8	3
Fish and insect larvae	1	0.8	4
Fish	12	1.9	5
Crayfish	2	1.6	5½
Fish and crayfish	3	3.1	6

SUMMARY

1. Burbot were sampled during studies of the Lake Winnipeg fishery from the catches of gill-nets, trap-nets and otter-trawl.
2. Ages were determined for 886 specimens using otoliths.
3. Fish from two localities were found to differ significantly in length-weight relationship.

4. Growth curves are presented for three groups of burbot. Exploitation probably accelerated the growth rate in one locality.

5. Samples from the trap-net and otter-trawl are more representative than those from gill-nets.

6. Some burbot are probably sexually mature when 2 years old, and immaturity seems to be associated more with size than with age.

7. Spawning begins about January 31 and lasts about 3 weeks. Some mature fish do not spawn every year.

8. The otter-trawl is better than gill-nets or trap-nets for taking burbot for stomach analysis.

9. Food consisted of insect larvae, crayfish and fish. Food preference of burbot was related to their size.

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CORRECTIONS FOR RECENT PUBLICATIONS OF THE
FISHERIES RESEARCH BOARD OF CANADA

BULLETINS OF THE FISHERIES RESEARCH BOARD OF CANADA

The title of Bulletin No. 96 should read:

Tagging of chum salmon in Johnstone Strait 1945 and 1950

JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

VOLUME XI, No. 5—paper by W. E. Ricker: "Stock and recruitment".

On page 610, starting at the end of the 8th line of the 2nd paragraph, the text should read:

This continues until all the thousand time-intervals have elapsed, at the end of which there are:

$$1,000,000(1 - 0.0008)^{1000} = 449,000$$

survivors (to the nearest thousand), or 44.9 per cent. What happens if the number of predators is doubled? In that event, during the first thousandth of the season twice as many fish will be eaten, i.e., 1,600, leaving 998,400. In the next thousandth the fraction eaten is likewise double, namely 0.0016; multiplied by the number of survivors this gives 1,597; and so on. At the end of the season $1,000,000(1 - 0.0016)^{1000}$ survive, which is 202,000, or 20.2 per cent.

Thus doubling the number of predators doubles the instantaneous mortality rate (which is true generally), but it increases the actual mortality from 55.1 to 79.8, or by only 45 per cent of its original value (which is true of only this particular example).

The same correction is needed in the article from which this excerpt was quoted (Canadian Fish Culturist, No. 13, on page 6).

VOLUME XI, No. 6—paper by Ralph V. Bangham and James R. Adams: "A survey of the parasites of freshwater fishes from the mainland of British Columbia".

Page 680, Species 2 (Rocky Mountain Whitefish): The fish from Jackfish Creek in the Liard Drainage, recorded as Rocky Mountain whitefish, are Arctic grayling.

Page 680, Species 3 (Round Whitefish): The specimens from Middle River in the Fraser Drainage are Rocky Mountain whitefish. No true round whitefish were examined.

The revised identifications of the above specimens were made by Dr. C. C. Lindsey.

On page 705, the 6th item under Trematoda should read: "*Bucephalopsis ozaki*".

VOLUME XI, No. 6—paper by R. W. Wolfgang: "Studies of the trematode *Stephanostomum baccatum* (Nicoll, 1907): II. Biology, with special reference to the stages affecting the winter flounder".

On pages 973 and 977, the legends for Figure 3 and Figure 7 have been interchanged.

VOLUME XII, No. 1—paper by J. M. Fraser: "The smallmouth bass fishery of South Bay, Lake Huron".

On page 171, line 10 of paragraph 2 should be deleted, and the following substituted:

catch. Therefore, if the sample examined from Jocko Bay is to truly represent its

VOLUME XII, No. 2—paper by L. M. Dickie and F. D. McCracken: "Isopleth diagrams to predict equilibrium yields of a small flounder fishery".

On page 195, the last paragraph should read:

A trial and error selection of $W_{\infty} = 2.38$ lb. (1079.5 g.) gave the best straight line fit to all the points, from which was obtained the equation:

$$\log_e(W_{\infty} - w_{(t-t_0)}) = 1.96 - 0.39(t - t_0)$$

whence,

$$W_{\infty} - w_{(t-t_0)} = 7.14e^{-0.39(t-t_0)}$$

VOLUME XII, No. 3—paper by M. P. Shepard: "Resistance and tolerance of young speckled trout (*Salvelinus fontinalis*) to oxygen lack, with special reference to low oxygen acclimation".

On page 421, formula (4) should read:

$$X^{a'} T_{50} = b'$$

Dr. D. W. M. Herbert has informed the author that this expression was proposed for the oxygen relationship by Mrs. K. M. Downing, rather than by Herbert and Merkens as indicated in the paper.

VOLUME XII, No. 4—paper by H. Godfrey: "On the ecology of Skeena River whitefishes, *Coregonus* and *Prosopium*".

On page 501, the redbelly dace, *Chrosomus eos*, is listed as a fish which occurs in the Skeena River drainage. This name was included on the basis of specimens taken in Morrison Lake (tributary to Babine Lake). The specimens have since been lost and it is impossible to confirm their identity. In British Columbia, *C. eos* has hitherto been reported only from Charlie Lake (Peace-Mackenzie system), Peace River district.

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Grainger, Edward Henry
6: 899

Gravel spawning beds
5: 706 (water seepage rate through)

Great Slave L.
5: 768 (inconnu)

Growth rate, age composition
1: 35 (albacore)
1: 93 (of sockeye in relation to parasitization)

1: 147 (smallmouth bass)
2: 187 (winter flounder)
2: 210 (of trout in relation to lake fertilization)

2: 238 (eels)
4: 487 (fishes of Ungava Crater and vicinity)

4: 497 (whitefishes of Skeena basin)
5: 768 (inconnu)
6: 930 (L. Winnipeg burbot)

Gulf of Mexico
5: 754 (new sturgeon)

Cuttman, Abraham

5: 637

Haddock (*Melanogrammus aeglefinus*)

3: 329 (spoilage assessment and quality standards)

5: 641 (liver extracts and hydrolysates)

Halibut, Atlantic and Pacific (*Hippoglossus*)

1: 85 (landings related to price and cost of living)

Halocline (*see also* density, salinity, oceanography)

1: 8 (B.C. offshore waters)

3: 352 (Miramichi Estuary, N.B.)

Hayes, Frederick Ronald

4: 618

Hemoglobin

6: 917 (in fish blood)

Herring, Atlantic (*Clupea harengus*)

1: 85 (landings related to price and cost of living)

Herring, Pacific (*Clupea pallasi*)

1: 85 (landings related to price and cost of living)

4: 571 (*Anisakis* infestation)

5: 649 (recruitment and mortality)

Hewson, Leo Clare

6: 930

Histology

1: 61 (albacore gonads)

1: 178 (pineal body of young sockeye)

Hoar, William Stewart

1: 178

Hudson Strait

5: 762 (barnacles)

6: 899 (echinoderms)

Humber Arm, Nfld.

5: 684 (sulphite pulp pollution survey)

Humidity, relative

1: 71 (effect on drying salted cod)

L. Huron

1: 147 (bass fishery, South Bay)

Hydrogen ion concentration (pH)

3: 333 (in quality assessment of haddock)

Hydrography (*see also* Oceanography)

3: 351 (Miramichi Estuary, N.B.)

Hydrology (*see also* Hydrography)

3: 346 (Miramichi R., N.B.)

Inconnu (*Stenodus leucichthys mackenziei*)

5: 768 (in Great Slave L., etc.)

Insects

4: 487 (from Ungava fishes)

Iron

5: 642 (in fish and mammalian livers)

Isentropic analysis

1: 22 (B.C. offshore waters)

Isopleths

1: 187 (of flounder yields, in pounds and in value)

6: 942 (correction)

Isotherm (*see also* limnology, oceanography)

1: 13 (B.C. offshore waters)

Ketchen, Keith Stuart

1: 134

Lactic acid

6: 899 (in blood of fishes after exercise)

Lea, Helen Elizabeth

4: 593

Legendre, Rosaire

1: 68

Length-weight relationships (*see* Morphometry)

Lethal limits

3: 387 (low oxygen, for trout)

6: 917 (temperature, oxygen, for various fishes)

Life history

1: 35 (Pacific albacore)

2: 238 (eels)

2: 287 (naticid whelks)

5: 781 (Brünnich's murre)

6: 797 (Bay of Fundy scallops)

6: 858 (Ungava Bay copepods)

Light, reactions to

1: 178 (effects of pineal injury)

2: 238 (eels in migration)

2: 270 (oyster larvae at spatting)

3: 369 (pink and chum salmon fry)

Limnology, physical

2: 210 (2 trout lakes of N.B.)

2: 238 (lakes containing eels)

4: 487 (Chubb Crater, P.Q.)

4: 499 (lakes of the Skeena basin)

4: 618 (Copper L., N.S.)

Ling (*see* burbot)

Liver

5: 637 (extracts and enzymic hydrolysates)

5: 642 (inorganic constituents)

5: 643 (organic nitrogen and vitamins)

Livingstone, Daniel Archibald

4: 618

Lobster

1: 85 (landings related to price and cost of living)

McCracken, Francis Derwood

2: 187; 6: 942

McKenzie, Russell Alderson

5: 698

MacKinnon, Dixon

3: 362

McLellan, Hugh John

3: 375

Mammals

2: 210 (in relation to trout, in N.B.)

4: 487 (near Ungava Crater)

Management, fishery

2: 187 (winter flounders)

2: 210 (trout lakes)

3: 451 (Skeena R. salmon)

4: 618 (trout in Copper L., N.S.)

Margolis, Leo

1: 97, 121

Maritime Provinces

1: 85 (catches of commercial fishes)

2: 187 (flounder yield in St. Mary Bay, N.S.)

2: 210 (trout angling in southern N.B.)

2: 270 (oyster spatfall in Bras d'Or Lakes, N.S.)

2: 287 (distribution of whelks)

4: 618 (trout management, Copper L., N.S.)

5: 698 (cod populations)

5: 754 (sea sturgeon)

6: 797 (giant scallop, Bay of Fundy)

Martin, Nigel Vernon

4: 487

Medcof, John Carl

2: 270

Migration and dispersion

1: 35 (Pacific albacore)

1: 147 (smallmouth bass)

2: 210 (of trout from lakes)

2: 238 (of eels into and out of lakes)

3: 362 (fry of Pacific salmon)

3: 369 (fry of pink and chum salmon)

Milne, Donald Johnston

3: 451

Mineral constituents

5: 642 (fish and mammalian livers)

Miramichi Estuary

3: 342 (hydrographic physical features)

Morphology (*see also* Morphometry, Histology)

1: 97 (whale helminths)

1: 121 (whale-lice)

1: 143 (folliculinid Ciliates)

4: 593 (Chaetognatha)

5: 742 (Kamloops trout)

5: 754 (sturgeons)

6: 858 (plankton copepods)

6: 899 (echinoderms)

Morphometry (*see also* Morphology)

1: 93 (parasitized and unparasitized sock-eye smolts)

5: 754 (sturgeons)

5: 768 (inconnu)

5: 781 (Ungava Bay fishes)

6: 930 (burbot)

Murre, Brünnich's

5: 781 (food)

Muscle proteins

1: 75 (of Atlantic cod)

5: 646 (of sturgeon)

Natural mortality

2: 187 (winter flounder)

2: 210 (of trout as affected by predator control)

5: 649 (B.C. herring)

6: 781 (scallop larvae)

Neave, Ferris

3: 369

Neelin, James Michael

1: 75

Nematoda

1: 93 (in sockeye smolts)

1: 97 (in whales)

4: 571 (in B.C. herring)

Newfoundland

5: 682 (sulphite pulp pollution survey)

Niacin

5: 643 (in fish and mammalian liver)

Nitrite

3: 340 (effect on trimethylamine production in haddock)

Nitrogenous constituents

5: 643 (in fish and mammalian livers)

5: 646 (in sturgeon muscle)

Obituary

6: 795 (G. B. Reed)

Oceanography, Atlantic

- 2: 270 (Gillis Cove, Bras d'Or Lake, N.S.)
- 3: 342 (Miramichi Estuary, N.B.)
- 3: 375 (Scotian Shelf)
- 5: 684 (Humber Arm, Nfld.)
- 6: 781 (relation to scallop survival)

Oceanography, Pacific

- 1: 1 (offshore waters)
- 4: 593 (related to distribution of arrow-worms)

Odour

- 3: 333 (in quality assessment of haddock)

Offshore waters

- 1: 1 (B.C. oceanography)
- 3: 375 (Scotian Shelf bottom temperatures)

Oxygen, dissolved (*see also* Limnology, Oceanography, Pollution)

- 1: 9 (B.C. offshore waters)
- 5: 706 (in gravel spawning beds)

Oxygen, reaction to

- 3: 387 (resistance and tolerance of trout)
- 4: 618 (speckled trout)
- 6: 899 (lethal levels after exercise, for various fishes)
- 6: 942 (correction)

Oysters, Atlantic

- 2: 270 (spatfall and larval behaviour)

Pantothenic acid

- 5: 643 (in fish and mammalian liver)

Parasites (*see* Nematoda, Trematoda, Whale-lice)

Parker, Richard Alan

- 3: 447

Partlo, John Middleton

- 1: 35, 61

Permeability of gravel spawning beds

- 5: 706 (measurement and theory)

Petersen estimates (*see* Abundance)pH (*see* Hydrogen ion concentration)

Phosphorus

- 5: 642 (in fish and mammalian livers)

Phototaxis (*see* Light, reactions to)

Physiology, circulatory

- 6: 917 (effect of activity on blood of freshwater fishes)

Physiology, digestive

- 5: 781 (conversion of food by murre)

Pigmentation

- 1: 178 (effect of pineal injury)

Pike, Gordon Chesley

- 1: 97

Pineal organ

- 1: 178 (effects of injury on sockeye smolts)

Plankton

- 4: 487 (Ungava Crater and neighbouring lakes)
- 6: 858 (Ungava Bay copepods)

Poisoning

- 4: 618 (Copper L., N.S.)

Pollard, Robert Anthony

- 5: 706

Pollution survey

- 5: 682 (sulphite pulp, Nfld.)

Pork

- 5: 641 (liver extracts and hydrolysates)

Predators

- 2: 210 (control on trout lakes)
- 4: 499 (of Skeena whitefishes)
- 4: 543 (fish in lakes)
- 5: 781 (murre, Ungava Bay)

Proteins

- 1: 75 (of Atlantic cod muscle)
- 5: 646 (of sturgeon muscle)

Pseudomonas

- 3: 337 (in spoilage of haddock)

Pseudocalanus minutus

- 6: 858 (Ungava Bay)

Pulp, sulphite

- 5: 682 (pollution survey, Nfld.)

Pumpkinseed sunfish (*Lepomis gibbosus*)

- 3: 447 (population estimate)

Pyramid of numbers

- 4: 543 (in lakes)

Quality tests

- 3: 333 (for freshness of haddock)

Raymond, Marcel

- 4: 496

Recruitment

- 1: 187 (St. Mary Bay winter flounders)
- 3: 447 (removal of effects on population estimates)
- 5: 649 (B.C. herring)
- 6: 941 (correction for paper)

Reed, Guilford Bevil

- 6: 795 (obituary)

Reproduction

- 6: 781 (scallop)
- 6: 930 (L. Winnipeg burbot)

Riboflavin

- 5: 643 (in fish and mammalian liver)

Ricker, William Edwin

- 6: 941

Rousseau, Jacques

4: 496

Salinity (*see also* oceanography)

3: 9 (B.C. offshore waters)

3: 352 (Miramichi Estuary, N.B.)

Salmon, Atlantic (*Salmo salar*)

5: 641 (liver extracts and hydrolysates)

Salmon, chinook or spring (*Oncorhynchus tshawytscha*)

3: 362 (movement of fry)

3: 451 (Skeena R. fishery)

Salmon, chum (*Oncorhynchus keta*)

3: 362 (movement of fry through impoundment)

3: 369 (seaward migration)

3: 451 (Skeena R. fishery)

6: 941 (correction of title)

Salmon, coho (*Oncorhynchus kisutch*)

3: 362 (movement of fry)

3: 451 (Skeena R. fishery)

Salmon, pink (*Oncorhynchus gorbuscha*)

3: 362 (movement of fry through impoundment)

3: 369 (seaward migration)

3: 451 (Skeena R. fishery)

Salmon, sockeye (*Oncorhynchus nerka*)

1: 93 (helminths in smolts)

1: 178 (phototaxis and pigmentation following pineal injury)

3: 362 (movement of fry)

3: 451 (Skeena R. fishery)

Salmon, Pacific (*Oncorhynchus* spp.)

1: 85 (landings related to price and cost of living)

Salmon spawning beds

5: 706 (water seepage rate through)

Salt fish

1: 68 (drying (cod))

Saunders, John Wilfred

2: 238

Scallop, giant

6: 797 (abundance in Bay of Fundy)

Scotian Shelf

3: 375 (bottom temperatures)

Seal, harp (*Phoca groenlandica*)

5: 641 (liver extracts and hydrolysates)

Seepage rate, measuring and theory

5: 706 (through gravel spawning beds)

Shepard, Michael Perry

3: 387; 6: 942

Skeena R.

3: 451 (salmon fishery)

4: 499 (freshwater fishes of the watershed)

Smith, George Francis Maurice

5: 698

Smith, Morden Whitney

2: 210, 238

Smith, Stuart Boland

5: 742

Sole, lemon (*Parophrys vetulus*)

1: 134 (corrosion of tags on)

Spawning beds, salmon

5: 706 (water seepage rate through)

Spermatozoa

1: 61 (albacore)

Spoilage

3: 329 (haddock, assessment of)

Squawfish (*Ptychocheilus oregonense*)

4: 499 (in lakes of the Skeena basin)

6: 899 (effects of exercise on blood)

Squires, Hubert Jacob

5: 781

Standing crop, of fishes

4: 543 (in lakes)

Stocking (of hatchery-reared fish)

2: 210 (trout in N.B. lakes)

Sturgeon (*Acipenser oxyrinchus*)

5: 646 (albumin protein of flesh)

5: 754 (new subspecies)

Sucker, coarse-scaled (*Catostomus macrocheilus*)

4: 499 (in lakes of the Skeena basin)

Sucker, fine-scaled (*Catostomus catostomus*)

4: 499 (in lakes of the Skeena basin)

6: 899 (effects of exercise on blood)

Sulphite pulp effluent

5: 685 (pollution survey, Nfld.)

Tagging and marking

1: 134 (corrosion of tagging wire)

2: 210 (of stocked fingerling trout)

6: 781 (scallop)

Taxonomy and systematics

1: 97 (whale helminths)

1: 121 (Amphipoda—Cyamidae)

1: 143 (Ciliata—Folliculinidae)

2: 287 (Gastropoda—Naticidae)

4: 593 (Chaetognatha)

5: 754 (Atlantic sturgeons)

5: 768 (inconnu)

5: 781 (fishes, invertebrates, Ungava Bay)

6: 858 (Copepoda—Ungava Bay)

Temperature, reaction to

- 4: 618 (speckled trout)
- 6: 781 (relation to scallop abundance)
- 6: 899 (lethal levels after exercise, various fishes)

Temperature, water (*see also* Limnology, Oceanography, Hydrography)

- 1: 11 (B.C. offshore waters)
- 3: 350, 354 (Miramichi R. and Estuary, N.B.)
- 3: 375 (Scotian Shelf bottom temperatures)

Tester, Albert Lewis

- 5: 649

Thiamin

- 5: 643 (in fish and mammalian liver)

Transparency of water

- 3: 355 (Miramichi Estuary, N.B.)

Trematoda

- 1: 97 (in whales)
- 6: 941, 942 (corrections)

Triggs, Rosalie Elizabeth

- 3: 329

Trimethylamine

- 3: 333 (in quality assessment of haddock)

Trimethylamine oxide

- 5: 646 (absence from sturgeon muscle)

Trout, cutthroat (*Salmo clarki*)

- 4: 499 (in lakes of the Skeena basin)

Trout, Kamloops (*Salmo gairdneri kamloops*)

- 5: 742 (scale-body relationship)
- 6: 899 (effects of exercise on blood)

Trout, lake (*Salvelinus namaycush*)

- 4: 487 (in Ungava)
- 4: 499 (in lakes of the Skeena basin)

Trout, speckled (*Salvelinus fontinalis*)

- 2: 210 (in lakes near St. Andrews, N.B.)
- 3: 387 (resistance and tolerance to reduced oxygen)
- 4: 618 (management in Copper L., N.S.)

Tuck, Leslie Mills

- 5: 781

Ungava Bay

- 5: 762 (barnacles)
- 6: 858 (copepods)
- 6: 899 (echinoderms)

Ungava Crater, P.Q.

- 4: 487

Upwelling

- 1: 23 (B.C. offshore waters)

Vavasour, Gerald Ralph

- 5: 682

Velella

- 1: 13 (off B.C. coast)

Vitamin B-complex and B₁₂

- 5: 643 (in fish and mammalian liver)

Vladykov, Vadim Dmitrovich

- 5: 754

Whales

- 1: 97 (helminth parasites of)
- 1: 121 (whale-lice)
- 5: 641 (liver extracts and hydrolysates)

Whale-lice (Amphipoda, Cyamidae)

- 1: 121 (taxonomy and synonymy)

Whitefish, common (*Coregonus clupeaformis*)

- 4: 499 (in Skeena drainage)

Whitefish, Rocky Mountain (*Prosopium wil-*
liamsoni)

- 4: 499 (in Skeena drainage)

Wind, effects of

- 1: 4 (B.C. offshore waters)
- 3: 351 (Miramichi Estuary, N.B.)

L. Winnipeg

- 6: 930 (burbot)

Wire

- 1: 134 (used for tagging)

Wisconsin

- 3: 447 (estimate of fish population in
Flora L.)

Wolfgang, Robert William

- 6: 942

